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Migratory locust

The **migratory locust** (*Locusta migratoria*) is the most widespread locust species, and the only species in the genus *Locusta*. It occurs throughout Africa, Asia, Australia and New Zealand. It used to be common in Europe but has now become rare there. Because of the vast geographic area it occupies, which comprises many different ecological zones, numerous subspecies have been described. However, not all experts agree on the validity of some of these subspecies.

Many other species of grasshopper with gregarious and possibly migratory behaviour are referred to as 'locusts' in the vernacular, including the widely distributed desert locust.

At 6.5 Gbp,[1] the migratory locust possesses the largest known insect genome.[2]

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Polyphenism

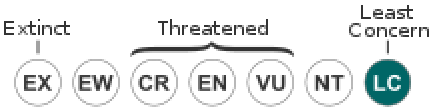
The migratory locust is polyphenic. It transitions between two main phenotypes in response to population density; the solitary phase and the gregarious phase. As the density of the population increases the locust transforms progressively from the solitary phase towards the gregarious phase with intermediate phases:

> Solitaire = solitary phase → transiens congregans (intermediate form) → gregarious phase → transiens dissocians (intermediate form) → solitaire = solitary phase.

Migratory locust

Female migratory locust

Conservation status



Least Concern (IUCN 3.1)

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Orthoptera
Suborder:	Caelifera
Family:	Acrididae
Subfamily:	Oedipodinae
Genus:	*Locusta* Linnaeus, 1758
Species:	***L. migratoria***

Binomial name

Locusta migratoria
(Linnaeus, 1758)

Synonyms

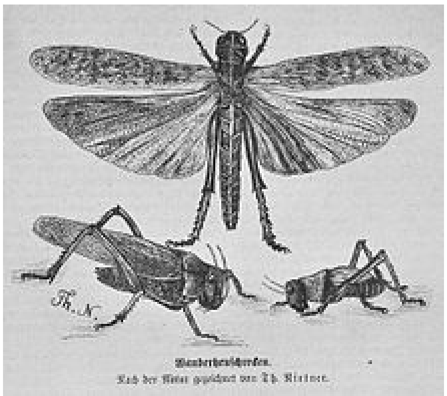
- *Acridium migratorium*
- *Acridium plorans*

Pigmentation and size of the migratory locust vary according to its phase (gregarious or solitary form) and its age. Gregarious larvae have a yellow to orange covering with black spots; solitary larvae are green or brown. The gregarious adult is brownish with yellow, the latter colour becoming more intense and extensive on maturation. The solitary adult is brown with varying extent of green colour depending on the colour of the vegetation. Gregarious adults vary in size between 40 and 60 mm according to the sex; they are smaller than the solitary adults.

- *Pachytylus australis* (Saussure, 1884)
- *Pachytylus migratorius* (Linnaeus, 1758)
- *Pachytylus migratorioides* (Fairmaire & L.J. Reiche, 1849)

Relationship with humans

Economic impact


Adult female (top), adult male (bottom left), fifth instar nymph (bottom right)

Locusts are highly mobile, and usually fly with the wind at a speed of about 15 to 20 kilometres per hour (9.3 to 12.4 mph). Swarms can travel 5 to 130 km or more in a day. Locust swarms can vary from less than one square kilometre to several hundred square kilometres with 40 to 80 million individuals per square kilometre. An adult locust can consume its own weight (several grams) in fresh food per day. For every million locusts, one ton of food is eaten.

In Africa, the last serious widespread plague of *L. m. migratorioides* occurred from 1928 to 1942. Since then, environmental transformations have made the development of swarms from the African migratory locust unlikely. Nevertheless, potential outbreaks are constantly monitored as plagues can be devastating. The Malagasy migratory locust (*L. m. capito*) still regularly swarms (roughly twice every ten years). The desert locust, which is very similar to the African migratory locust, remains a major threat too.

Locust survey and control are primarily the responsibility of the Ministry of Agriculture in locust-affected countries and are operations undertaken by national locust units. The Food and Agriculture Organization (FAO) of the United Nations provides information on the general locust situation to all interested countries and gives warnings and forecasts to those countries in danger of invasion.

As food / edibility

The migratory locust is an edible insect.[3][4] In Europe, the migratory locust is officially approved for the use in food in Switzerland (since May 2017).[5]

Subspecies of *Locusta migratoria*

L. migratoria is found over a vast geographic area, and its range covers many different ecological zones. Because of this, numerous subspecies have been described; however, not all experts agree on the validity of some of these subspecies.[6]

- *L. m. burmana* Ramme, 1951
- *L. m. capito* Saussure, 1884 (Malagasy migratory locust: Madagascar)
- *L. m. cinerascens* Fabricius, 1781 (Italy, Spain)
- *L. m. manilensis* (Meyen, 1835) 1 (eastern Asia)
- *L. m. migratoria* (Linnaeus, 1758) (Eurasian migratory locust: West and Central Asia, eastern Europe)
- *L. m. migratorioides* (Fairmaire & L.J. Reiche, 1849) (African migratory locust: Africa and Atlantic islands)

- *L. m. tibetensis* Chen, Yonglin, 1963
- *L. m. danica* (Linnaeus, 1767) = *L. m. migratoria* (Linnaeus, 1758)
- *L. m. gallica* Remaudičre, 1947 = *L. m. migratoria* (Linnaeus, 1758)
- *L. m. solitaria* Carthy, 1955 = *L. m. migratoria* (Linnaeus, 1758)

L. m. migratorioides female (solitary)

L. m. migratorioides male (solitary)

Other species called 'locusts'

Other species of Orthoptera that display gregarious and migratory behaviour are called 'locusts'.

- American locust, *Schistocerca americana*
- Australian plague locust, *Chortoicetes terminifera*
- Bombay locust, *Nomadacris succincta*
- Brown locust, *Locustana pardalina*
- Desert locust, *Schistocerca gregaria*
- Egyptian locust, *Anacridium aegyptium*
- Italian locust, *Calliptamus italicus*
- Moroccan locust, *Dociostaurus maroccanus*
- Red locust, *Nomadacris septemfasciata*
- Rocky Mountain locust, *Melanoplus spretus* – extinct
- Sahelian tree locusts, *Anacridium melanorhodon*
- Spur-throated locust, *Austracris guttulosa* (note: "spur-throated grasshoppers/locusts" may also refer to spp. in other genera)
- Sudan plague locust, *Aiolopus simulatrix*

The Senegalese grasshopper (*Oedaleus senegalensis*) also often displays locust-like behaviour in the Sahel region.

Photos

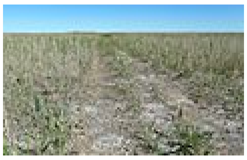
First instar nymph (gregarious)

Second and fourth instar nymphs (gregarious)

Third instar nymphs (gregarious)

Fourth instar nymph (gregarious)

Part of a hopper band in Kazakhstan



Hopper band in Kazakhstan

See also

- 2004 locust outbreak
- 2013 Madagascar locust infestation
- Australian Plague Locust Commission (APLC)

Footnotes

1. Wang, Xianhui; Fang, Xiaodong; Yang, Pengcheng; Jiang, Xuanting; Jiang, Feng; Zhao, Dejian; Li, Bolei; Cui, Feng; Wei, Jianing; Ma, Chuan; Wang, Yundan; He, Jing; Luo, Yuan; Wang, Zhifeng; Guo, Xiaojiao; Guo, Wei; Wang, Xuesong; Zhang, Yi; Yang, Meiling; Hao, Shuguang; Chen, Bing; Ma, Zongyuan; Yu, Dan; Xiong, Zhiqiang; Zhu, Yabing; Fan, Dingding; Han, Lijuan; Wang, Bo; Chen, Yuanxin; Wang, Junwen; Yang, Lan; Zhao, Wei; Feng, Yue; Chen, Guanxing; Lian, Jinmin; Li, Qiye; Huang, Zhiyong; Yao, Xiaoming; Lv, Na; Zhang, Guojie; Li, Yingrui; Wang, Jian; Wang, Jun; Zhu, Baoli; Kang, Le (2014). "The locust genome provides insight into swarm formation and long-distance flight" (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3896762). *Nature Communications*. **5**: 2957. doi:10.1038/ncomms3957 (https://doi.org/10.1038%2Fncomms3957). ISSN 2041-1723 (https://www.worldcat.org/issn/2041-1723). PMC 3896762 (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3896762). PMID 24423660 (https://www.ncbi.nlm.nih.gov/pubmed/24423660).
2. Li, Sheng; Zhu, Shiming; Jia, Qiangqiang; Yuan, Dongwei; Ren, Chonghua; Li, Kang; Liu, Suning; Cui, Yingying; Zhao, Haigang; Cao, Yanghui; Fang, Gangqi; Li, Daqi; Zhao, Xiaoming; Zhang, Jianzhen; Yue, Qiaoyun; Fan, Yongliang; Yu, Xiaoqiang; Feng, Qili; Zhan, Shuai (2018). "The genomic and functional landscapes of developmental plasticity in the American cockroach" (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5861062). *Nature Communications*. **9** (1): 1008. doi:10.1038/s41467-018-03281-1 (https://doi.org/10.1038%2Fs41467-018-03281-1). ISSN 2041-1723 (https://www.worldcat.org/issn/2041-1723). PMC 5861062 (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5861062). PMID 29559629 (https://www.ncbi.nlm.nih.gov/pubmed/29559629). This article contains quotations from this source, which is available under the Creative Commons Attribution 4.0 International (CC BY 4.0) (https://creativecommons.org/licenses/by/4.0/) license

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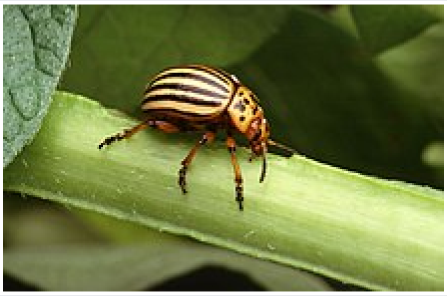
Colorado potato beetle

The **Colorado potato beetle** (*Leptinotarsa decemlineata*), also known as the **Colorado beetle**, the **ten-striped spearman**, the **ten-lined potato beetle** or the **potato bug**, is a major pest of potato crops. It is approximately 10 millimetres (0.39 in) long, with a bright yellow/orange body and five bold brown stripes along the length of each of its elytra. Native to America, it spread rapidly in potato crops across America and then Europe from 1859 onwards.

Colorado potato beetle



Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Coleoptera
Family:	Chrysomelidae
Genus:	*Leptinotarsa*
Species:	***L. decemlineata***

Binomial name

Leptinotarsa decemlineata
Say, 1824[1]

Synonyms[2]

- *Doryphora decemlineata* Say, 1824
- *Stilodes decemlineata*

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- **Description**
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- **As an agricultural pest**
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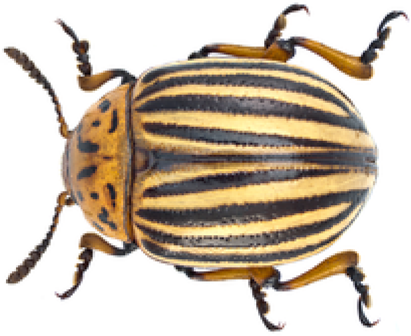
Taxonomy

The Colorado potato beetle was first observed in 1811 by Thomas Nuttall and was formally described in 1824 by the American entomologist Thomas Say.[3] The beetles were collected in the Rocky Mountains where they were feeding on the buffalo bur, *Solanum rostratum*.[4] The genus *Leptinotarsa* is assigned to the chrysolmelid beetle tribe *Doryphorini* (located in subfamily Chrysomelinae), which it shares with five other *genera*: *Doryphora*, *Calligrapha*, *Labidomera*, *Proseicela*, and *Zygogramma*.[5]

Description

Adult beetles average 6–11 millimetres (0.24–0.43 in) in length and 3 millimetres (0.12 in) in width. The beetles are orange-yellow in colour with ten characteristic black stripes on the elytra. The species name *decemlineata*, meaning 'ten-lined', derives from this feature.[4][6] Adult beetles may, however, be visually confused with *L. juncta*, the false potato beetle, which is not an agricultural pest. *L. juncta* also has alternating black and white strips on its back, but one of the white strips in the center of each wing cover is missing and replaced by a light brown strip.[7]

The orange-pink larvae have a large, nine segmented, abdomen and black head, prominent spiracles and may measure up to 15 millimetres (0.59 in) in length in their final instar stage. The beetle larva has four instar stages. The head remains black throughout these stages, but the pronotum changes colour from black in first- and second-instar larvae to having an orange-brown edge in its third-instar. In fourth-instar larvae, about half the pronotum is coloured light brown.[4][8] This tribe is characterised within the subfamily by round to oval shaped convex bodies which are usually brightly coloured, simple claws which separate at the base, open cavities behind the procoxae, and a variable apicial segment of the maxillary palp.[9][6]



Leptinotarsa decemlineata adult specimen

Distribution

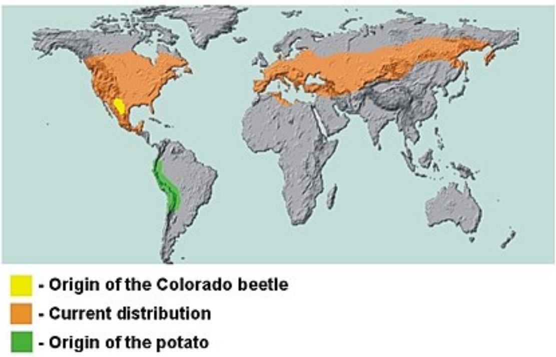
The beetle is native to North America, and is present in every state and province except Alaska, California, Hawaii, and Nevada.[4] It now has a wide distribution across Europe and Asia,[10] totalling over 16 million km^2.[11]

Its first association with the potato plant (*Solanum tuberosum*) was not made until about 1859 when it began destroying potato crops in the region of Omaha, Nebraska. Its spread eastward was rapid, at an average distance of 140 km per year.[12] By 1874 it had reached the Atlantic Coast.[4] From 1871, the American entomologist Charles Valentine Riley warned Europeans about the potential for an accidental infestation caused by the transportation of the beetle from America.[12] From 1875, several western European countries, including Germany, Belgium, France and Switzerland, banned imports of American potatoes to avoid infestation by *L. decemlineata*.[13]

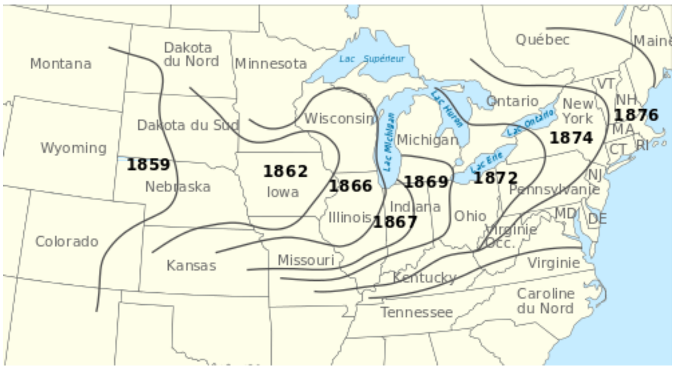
These controls proved ineffective as the beetle soon reached Europe. In 1877, *L. decemlineata* reached the United Kingdom and was first recorded from Liverpool docks, but it did not become established. There have been many further outbreaks: the species has been eradicated in the UK at least 163 times. The last major outbreak was in 1976. It remains as a notifiable quarantine pest in the United Kingdom and is monitored by DEFRA to prevent it from becoming established.[14] A cost-benefit analysis from 1981 suggested that the cost of the measures used to exclude *L. decemlineata* from the UK was less than the likely costs of control if it became established.[15]

Elsewhere in Europe, the beetle became established near USA military bases in Bordeaux during or immediately following World War I and had proceeded to spread by the beginning of World War II to Belgium, the Netherlands and Spain. The population increased dramatically during and immediately following World War II and spread eastward, and the beetle is now found over much of the continent. After World War II, in the Soviet occupation zone of Germany, almost half of all potato fields were infested by the beetle by 1950. In East Germany they were known as *Amikäfer* ('Yankee beetles') following a governmental claim that the beetles were dropped by American planes. In the EU it remains a regulated (quarantine) pest for the UK, Republic of Ireland, Balearic Islands, Cyprus, Malta and southern parts of Sweden and Finland. It is not established in any of these Member States, but occasional infestations can occur when, for example, wind blows adults from Russia to Finland.[16][17]

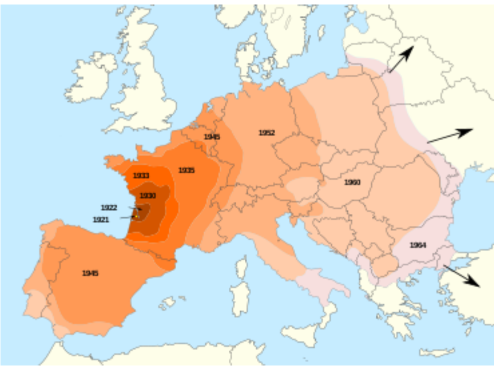
The beetle has the potential to spread to temperate areas of East Asia, India, South America, Africa, New Zealand, and Australia.[18]



Native range of the potato and native and current range of the Colorado beetle.



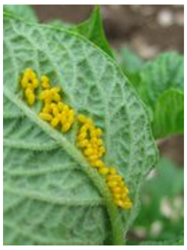
Expansion of the Colorado potato beetle's range in North America, 1859–1876.

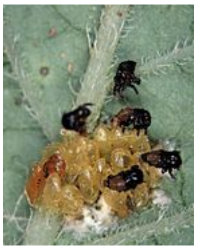


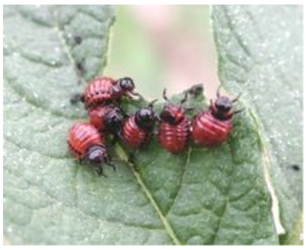
Expansion of the Colorado potato beetle's range in Europe, 1921–1964.

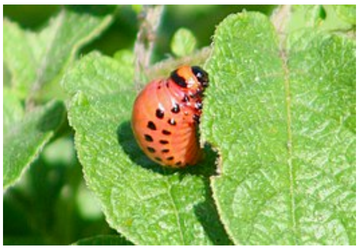
Lifecycle

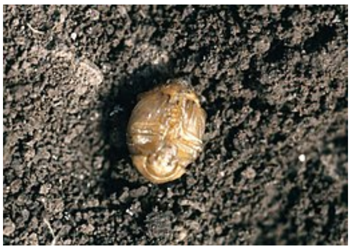
Colorado potato beetle females are very prolific and are capable of laying over 500 eggs in a 4- to 5-week period.[19] The eggs are yellow to orange, and are about 1 mm (0.039 in) long. They are usually deposited in batches of about 30 on the underside of host leaves. Development of all life stages depends on temperature. After 4–15 days, the eggs hatch into reddish-brown larvae with humped backs and two rows of dark brown spots on either side. They feed on the leaves of their host plant. Larvae progress through four distinct growth stages (instars). First instars measure approximately 1.50 mm (0.059 in) long, and the last (fourth) instars measure 8 mm (0.31 in) in length. The first through third instars each last about 2–3 days duration; the fourth lasts 4–7 days. Upon reaching full size, each fourth instar spends several days as a nonfeeding prepupa, which can be recognized by its inactivity and lighter coloration. The prepupae drop to the soil and burrow to a depth of several inches, then pupate.[4] In 5 to 10 days, the adult beetle emerges to feed and mate. This beetle can thus go from egg to adult in as little as 21 days.[19] Depending on temperature, light conditions, and host quality, the adults may enter diapause and delay emergence until spring. They then return to their host plants to mate and feed; overwintering adults may begin mating within 24 hours of spring emergence.[20] In some locations, three or more generations may occur each growing season.[4]

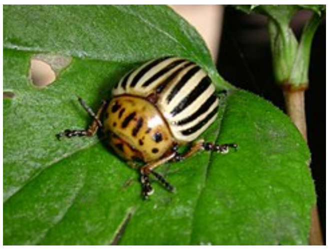

Eggs laid on the underside of a leaf


First-instar larva after hatching


Early (3rd) instar stage of larvae


Late (4th) instar stage of larva, before pupation


Pupa


Adult beetle after emergence

Mating adult beetles

Behavior and ecology

Diet

L. decemlineata has a strong association with plants in the family Solanaceae, particularly those of the genus *Solanum*. It is directly associated with *Solanum cornutum* (buffalo-bur), *Solanum nigrum* (black nightshade), *Solanum melongena* (eggplant or aubergine), *Solanum dulcamara* (bittersweet nightshade), *Solanum luteum* (hairy nightshade), *Solanum tuberosum* (potato), and *Solanum elaeagnifolium* (silverleaf nightshade). They are also associated with other plants in this family, namely the species *Solanum lycopersicum* (tomato) and the genus *Capsicum* (pepper).[21]

Predators

At least 13 insect genera, three spider families, one phalangid (Opiliones), and one mite have been recorded as either generalist or specialized predators of the varying stages of *L. decemlineata*. These include the ground beetle *Lebia grandis*, the Coccinellid beetles *Coleomegilla maculata* and *Hippodamia convergens*, the shield bugs *Perillus bioculatus* and *Podisus maculiventris*, as well as various species of the lacewing genus *Chrysopa*, the wasp genus *Polistes*, and the damsel bug genus *Nabis*.[22]

Coleomegilla maculata preying upon Colorado beetle eggs

The predatory ground beetle *L. grandis* is a predator of both the eggs and larvae of *L. decemlineata*, and its larvae are parasitoids of the pupae. An adult *L. grandis* may consume up to 23 eggs or 3.3 larvae in a single day.[23]

In a laboratory experiment, *Podisus maculiventris* was used as a predatory threat to female *L. decemlineata* specimens, resulting in the production of unviable trophic eggs alongside viable ones; this response to a predator ensured that additional food was available for newly hatched offspring in order to increase their survival rate. The same experiment also demonstrated the cannibalism of unhatched eggs by newly hatched *L. decemlineata* larvae as an anti-predator response.[24]

Examples of parasitoids, predators, and pathogens of different life stages of *Leptinotarsa decemlineata* 1

Type	Species	Order	Predates	Location	Reference
Parasitoid	*Chrysomelobia labidomerae*	Acari	Adults	USA, Mexico	[25]
	Edovum puttleri	Hymenoptera	Eggs	USA, Mexico, Colombia	[26]
	Anaphes flavipes	Hymenoptera	Eggs	USA	
	Myiopharus aberrans	Diptera	Eggs	USA	
	Myiopharus doryphorae	Diptera	Larvae	USA, Canada	
	Meigenia mutabilis	Diptera	Larvae	Russia	
	Megaselia rufipes	Diptera	Adults	Germany	
	Heterorhabditis bacteriophora	Nematoda	Adults	Cosmopolitan	[27]
	Heterorhabditis heliothidis	Nematoda	Adults	Cosmopolitan	
Predator	*Lebia grandis*	Coleoptera	Eggs, Larvae, Adults	USA	
	Hippodamia convergens	Coleoptera	Eggs, Larvae	USA, Mexico	
	Euthyrhynchus floridanus	Hemiptera	Larvae	USA	[28]
	Oplomus dichrous	Hemiptera	Eggs, Larvae	USA, Mexico	[29]
	Perillus bioculatus	Hemiptera	Eggs, Larvae, Adults	USA, Mexico, Canada	[30]
	Podisus maculiventris	Hemiptera	Larvae	USA	[31]
	Pselliopus cinctus	Hemiptera	Larvae	USA	
	Sinea diadema	Hemiptera	Larvae	USA	
	Stiretrus anchorago	Hemiptera	Larvae	USA, Mexico	
Pathogen	*Bacillus thuringiensis* subsp. *tenebrionis*	Bacteria	Larvae	USA, Canada, Europe	
	Photorhabdus luminescens	Bacteria	Adults, Larvae	Cosmopolitan	[32]
	Spiroplasma	Bacteria	Adults, Larvae	North America, Europe	[33]
	Beauveria bassiana	Hypocreales	Adults, Larvae	USA	[34]

As an agricultural pest

Potato crop pest

In about 1840, *L. decemlineata* adopted the cultivated potato into its host range and it rapidly became a most destructive pest of potato crops. They are today considered to be the most important insect defoliator of potatoes.[18] They may also cause considerable damage to tomato and eggplant crops with both adults and larvae feeding on the plant's foliage. Larvae may defoliate potato plants resulting in yield losses of up to 100% if the damage occurs prior to tuber formation.[35] Larvae may consume 40 cm^2 of potato leaves during the entire larval stage, but adults are capable of consuming 10 cm^2 of foliage per day.[36]

The economic cost of insecticide resistance is significant, but published data on the subject is minimal.[37] In 1994, total costs of the insecticide and crop losses in the US state of Michigan were $13.3 million, representing 13.7% of the total value of the crop. The estimate of the cost implication of insecticides and crop losses per hectare is $138–368. Long-term increased cost to the Michigan potato industry caused by insecticide resistance in Colorado potato beetle was estimated at $0.9 to $1.4 million each year.[38]

Play media

Dutch newsreel from 1947

Insecticidal management

The large scale use of insecticides in agricultural crops effectively controlled the pest until it became resistant to DDT in 1952 and dieldrin in 1958.[39] Insecticides remain the main method of pest control on commercial farms. However, many chemicals are often unsuccessful when used against this pest because of the beetle's ability to rapidly develop insecticide resistance. Different populations in different geographic regions have, between them, developed resistance to all major classes of insecticide,[40][41] although not every population is resistant to every chemical.[40] The species as a whole has evolved resistance to 56 different chemical insecticides.[42] The mechanisms used include improved metabolism of the chemicals, reduced sensitivity of target sites, less penetration and greater excretion of the pesticides, as well as some changes in the behavior of the beetles.[40]

Examples of insecticides available for the control of Colorado potato beetle on different crops in Kentucky, USA.[19]

Insecticide class	Common examples	Potato	Eggplant	Tomato	Notes
Organophosphates	phosmet	X			on US Emergency Planning List of Extremely Hazardous Substances
	disulfoton	X		X	Usage restricted by US government; manufacturer Bayer exited US market 2009
Carbamates	carbaryl	X	X	X	Widely used in US
	carbofuran	X			One of the most toxic carbamates
Chlorinated hydrocarbons	methoxychlor	X		X	Banned in EU 2002, in USA 2003
(Cycloldienes)	endosulfan	X	X	X	Acutely toxic, bioaccumulates, endocrine disruptor. Global ban 2012 with exemptions until 2017
Insect growth regulator	azadirachtin	X	X	X	
Spinosin	spinosad		X	X	
Avermectin	abamectin	X		X	

Non-pesticidal management

Bacterial insecticides can be effective if application is targeted towards the vulnerable early-instar larvae. Two strains of the bacterium *Bacillus thuringiensis* produce toxins which kill the larvae.[35] Other forms of pest control, through non-pesticidal management are available. Feeding can be inhibited by applying antifeedants, such as fungicides or products derived from Neem

(*Azadirachta indica*), but these may have negative effects on the plants as well.[35] The steam distillate of fresh leaves and flowers of tansy (*Tanacetum vulgare*) contains high levels of camphor and umbellulone and these chemicals are strongly repellent to *L. decemlineata*.[43]

East German Young Pioneers collecting beetles during the war against the potato beetle

Beauveria bassiana (Hyphomycetes) is a pathogenic fungus that infects a wide range of insect species, including the Colorado potato beetle.[44] It has shown to be particularly effective as a biological pesticide for *L. decemlineata* when used in combination with the bacterium *Bacillus thuringiensis*.[45]

Crop rotation is, however, the most important cultural control of *L. decemlineata*.[18] Rotation may delay the infestation of potatoes and can reduce the build-up of early season beetle populations because the adults emerging from diapause can only disperse to new food sources by walking.[35] One 1984 study showed that rotating potatoes with non-host plants reduced the density of early season adults by 95.8%.[46]

Other cultural controls may be used in combination with crop rotation: Mulching the potato crop with straw early in the growing season may reduce the beetle's ability to locate potato fields, and the mulch creates an environment that favours beetle's predators; Plastic-lined trenches have been used as pitfall traps to catch the beetles as they move toward a field of potatoes in the spring, exploiting their inability to fly immediately after emergence; Flamethrowers may also be used to kill the beetles when they are visible at the top of the plant's foliage.[47]

Relationship with humans

Cold War villain

During the Cold War it was claimed by some countries in the Warsaw Pact that the beetles had been introduced by the CIA in an attempt to reduce food security by destroying the agriculture of the Soviet Union.[48] A widespread campaign was launched against the beetles; posters were put up and school children were mobilized to gather the pests and drown them in benzene or spirit.[48]

Philately

L. decemlineata is an iconic species and has been used as an image on stamps because of its association with the recent history of both North America and Europe. For example, in 1956, Romania issued a set of four stamps calling attention to the campaign against insect pests[50] and it was featured on a 1967 stamp issued in Austria.[51] The beetle also appeared on stamps issued in Benin, Tanzania, the United Arab Emirates, and Mozambique.[52]

Statue of the Colorado potato beetle in Hédervár, Hungary. It marks the discovery of the beetle at the site in 1947 during the rapid spread of the pest in Europe throughout the 20th century.[49]

In popular culture

During the 2014 pro-Russian unrest in Ukraine, the word *kolorady*, from the Ukrainian and Russian term for Colorado beetle, (Ukrainian: жук колорадський, Russian: колорадский жук) gained popularity among Ukrainians as a derogatory term to describe pro-Russian separatists in the

Donetsk and Luhansk Oblasts (provinces) of Eastern Ukraine. The nickname reflects the similarity of black and orange stripes on so-called St. George's ribbons worn by many of the separatists.[53]

Notes

1. **^** For a more comprehensive list of natural predators, pathogens and parasitoids, see here (http://www.cabi.org/isc/datasheet/30380).

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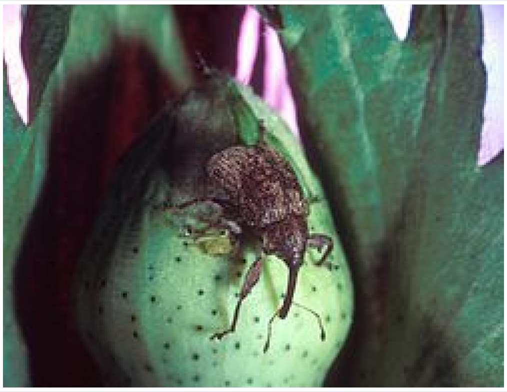
Boll weevil

The **boll weevil** (*Anthonomus grandis*) is a beetle which feeds on cotton buds and flowers. Thought to be native to Central Mexico,[1] it migrated into the United States from Mexico in the late 19th century and had infested all U.S. cotton-growing areas by the 1920s, devastating the industry and the people working in the American South. During the late 20th century, it became a serious pest in South America as well. Since 1978, the Boll Weevil Eradication Program in the U.S. allowed full-scale cultivation to resume in many regions.

Boll weevil



Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Coleoptera
Family:	Curculionidae
Subfamily:	Curculioninae
Tribe:	Anthonomini
Genus:	*Anthonomus*
Species:	***A. grandis***

Binomial name

Anthonomus grandis
Boheman, 1843

Contents

- **Description**
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- **Infestation**
- **Control**
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Description

The adult insect has a long snout, is grayish color, and is usually less than 6 mm long.

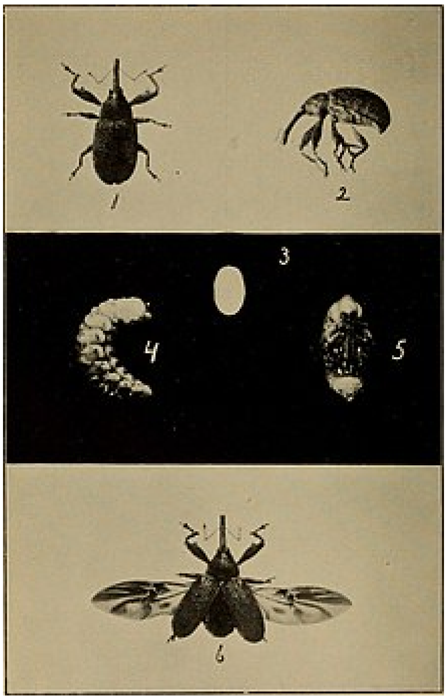
Lifecycle

Adult weevils overwinter in well-drained areas in or near cotton fields, and farms after diapause. They emerge and enter cotton fields from early spring through midsummer, with peak emergence in late spring, and feed on immature cotton bolls.

The boll weevil lays its eggs inside buds and ripening bolls (fruits) of the cotton plants. The female can lay up to 200 eggs over a 10- to 12-day period. The oviposition leaves wounds on the exterior of the flower bud. The eggs hatch in 3 to 5 days within the cotton squares (larger buds before flowering), feed for 8 to 10 days, and finally pupate. The pupal stage lasts another 5 to 7 days. The lifecycle from egg to adult spans about three weeks during the summer. Under optimal conditions, 8 to 10 generations per season may occur.

Boll weevils begin to die at temperatures at or below −5 °C (23 °F). Research at the University of Missouri indicates they cannot survive more than an hour at −15 °C (5 °F). The insulation offered by leaf litter, crop residues, and snow may enable the beetle to survive when air temperatures drop to these levels.

Other limitations on boll weevil populations include extreme heat and drought. Its natural predators include fire ants, insects, spiders, birds, and a parasitic wasp, *Catolaccus grandis*. The insects sometimes emerge from diapause before cotton buds are available.



1) Back view of adult; 2) side view of adult; 3) egg; 4) side view of larva; 5) ventral view of pupa; 6) adult, with wings spread

Infestation

The insect crossed the Rio Grande near Brownsville, Texas, to enter the United States from Mexico in 1892[2] and reached southeastern Alabama in 1909. By the mid-1920s, it had entered all cotton-growing regions in the U.S., travelling 40 to 160 miles per year. It remains the most destructive cotton pest in North America. Since the boll weevil entered the United States, it has cost U.S. cotton producers about $13 billion, and in recent times about $300 million per year.[2]

The boll weevil contributed to the economic woes of Southern farmers during the 1920s, a situation exacerbated by the Great Depression in the 1930s.

The boll weevil appeared in Venezuela in 1949 and in Colombia in 1950.[3] The Amazon Rainforest was thought to present a barrier to its further spread, but it was detected in Brazil in 1983, and an estimated 90% of the cotton farms in Brazil are now infested. During the 1990s, the weevil spread to Paraguay and Argentina. The International Cotton Advisory Committee has proposed a control program similar to that used in the U.S.[3]

Cotton boll with weevil larvae.

Control

During early years of the weevil's presence, growers sought relatively warm soils and early-ripening cultivars. Following World War II, the development of new pesticides such as DDT enabled U.S. farmers again to grow cotton as an economic crop. DDT was initially extremely effective, but U.S. weevil populations developed resistance by the mid-1950s.[4] Methyl parathion, malathion, and pyrethroids were subsequently used, but environmental and resistance concerns arose as they had with DDT, and control strategies changed.[4]

While many control methods have been investigated since the boll weevil entered the United States, insecticides have always remained the main control methods. In the 1980s, entomologists at Texas A&M University pointed to the spread of another invasive pest, the red imported fire ant, as a factor in the weevils' population decline in some areas.[5]

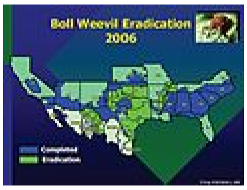
Other avenues of control that have been explored include weevil-resistant strains of cotton,[6] the parasitic wasp *Catolaccus grandis*,[7] the fungus *Beauveria bassiana*,[8] and the Chilo iridescent virus. Genetically engineered Bt cotton is not protected from the boll weevil.[9]

Although it was possible to control the boll weevil, to do so was costly in terms of insecticide costs. The goal of many cotton entomologists was to eventually eradicate the pest from U.S. cotton. In 1978, a large-scale test was begun in eastern North Carolina and in Southampton County, Virginia, to determine the feasibility of eradication. Based on the success of this test, area-wide programs were begun in the 1980s to eradicate the insect from whole regions. These are based on cooperative effort by all growers together with the assistance of the Animal and Plant Health Inspection Service of the United States Department of Agriculture (USDA).

Adult on a cotton boll

The program has been successful in eradicating boll weevils from all cotton-growing states with the exception of Texas, and most of this state is free of boll weevils. Problems along the southern border with Mexico have delayed eradication in the extreme southern portions of this state. Follow-up programs are in place in all cotton-growing states to prevent the reintroduction of the pest. These monitoring programs rely on pheromone-baited traps for detection. The boll weevil eradication program, although slow and costly, has paid off for cotton growers in reduced pesticide costs. This program and the screwworm program of the 1950s are among the biggest and most successful insect control programs in history.[10]

"Beat the boll weevil..." (U.S. Food Administration, Educational div., Advertising section, 1918-1919)



Eradication map (USDA, 2006)

Impact

The Library of Congress American Memory Project contains a number of oral history materials on the boll weevil's impact.[11]

A 2009 study found "that as the weevil traversed the American South [in the period 1892-1932], it seriously disrupted local economies, significantly reduced the value of land (at this time still the most important asset in the American South), and triggered substantial intraregional population movements."[12] A 2018 National Bureau of Economic Research paper found that the boll weevil spread between 1892 to 1922 had a beneficial impact on educational outcomes, as children were less likely to work on cultivating cotton.[13]

The boll weevil plaque in Enterprise, Alabama

The boll weevil infestation has been credited with bringing about economic diversification in the Southern US, including the expansion of peanut cropping. The citizens of Enterprise, Alabama, erected the Boll Weevil Monument in 1919, perceiving that their economy had been overly dependent on cotton, and that mixed farming and manufacturing were better alternatives.

The boll weevil is the mascot for the University of Arkansas at Monticello and is listed on several "silliest" or "weirdest" mascots of all time.[14][15] It was also the mascot of a short-lived minor league baseball team, the Temple Boll Weevils, which were alternatively called the "Cotton Bugs."

"Boll Weevil" is a traditional blues song which reached #2 on the Billboard chart in 1961.

In the original 1980s *Transformers* cartoon series, Decepticon character Bombshell's alternative form is loosely based on the boll weevil.

See also

- *Lixus concavus*, the rhubarb curculio weevil
- Female sperm storage

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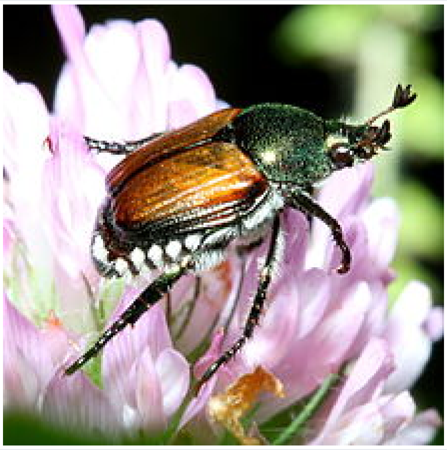
Japanese beetle

The **Japanese beetle** (*Popillia japonica*) is a species of scarab beetle. The adult measures 15 mm (0.6 in) in length and 10 mm (0.4 in) in width, has iridescent copper-colored elytra and a green thorax and head. It is not very destructive in Japan, where it is controlled by natural predators, but in North America, it is a noted pest of about 300 species of plants including rose bushes, grapes, hops, canna, crape myrtles, birch trees, linden trees, and others.

The adult beetles damage plants by skeletonizing the foliage, that is, consuming only the leaf material between the veins, and may also feed on fruit on the plants if present, while the subterranean larvae feed on the roots of grasses.

Japanese beetle



Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Coleoptera
Family:	Scarabaeidae
Genus:	*Popillia*
Species:	***P. japonica***

Binomial name

Popillia japonica

Newman, 1841

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Description

Adult *P. japonica* measure 15 mm (0.6 in) in length and 10 mm (0.4 in) in width, with iridescent copper-colored elytra and green thorax and head. A row of white tufts (spots) of hair project from under the wing covers on each side of the body.[1]

Distribution

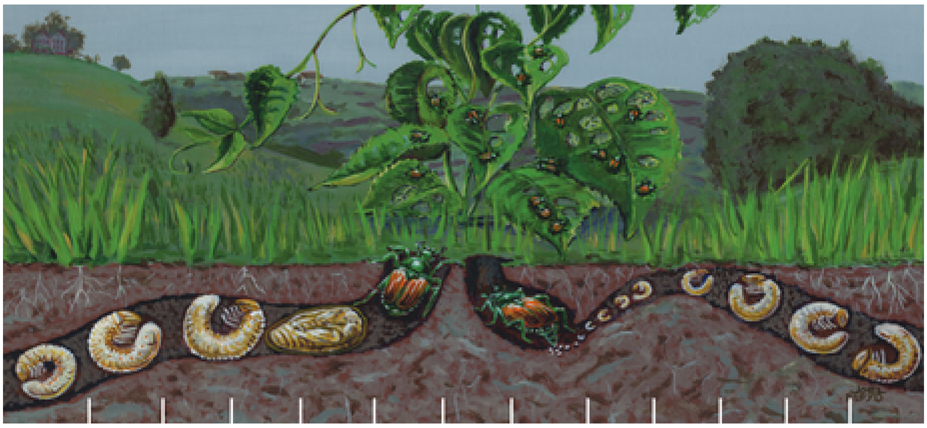
P. japonica is native to Japan, but is an invasive species in North America.

The first written evidence of the insect appearing within the United States was in 1916 in a nursery near Riverton, New Jersey.[2] The beetle larvae are thought to have entered the United States in a shipment of iris bulbs prior to 1912, when inspections of commodities entering the country began. As of 2015, only nine western US states were considered free of Japanese beetles.[3] Beetles have been detected in airports on the west coast of the United States since the 1940s.

The first Japanese beetle found in Canada was in a tourist's car at Yarmouth, arriving in Nova Scotia by ferry from Maine in 1939. During the same year, three additional adults were captured at Yarmouth and three at Lacolle in southern Quebec.[4]

Japanese beetles have been found in the islands of the Azores since the 1970s.[5] In 2014, the first population in mainland Europe was discovered near Milan in Italy.[6][7] In 2017 the pest was detected in Switzerland, most likely having spread over the border from Italy. Swiss authorities are attempting to eradicate the pest.[8]

Lifecycle



Lifecycle of the Japanese beetle. Larvae feed on roots underground, while adults feed on leaves and stems.

Ova are laid individually, or in small clusters near the soil surface.[9] Within approximately two weeks, the ova hatch, the larvae feeding on fine roots and other organic material. As the larvae mature, they become c-shaped grubs which consume progressively coarser roots and may do economic damage to pasture and turf at this time.

Larvae hibernate in small cells in the soil, emerging in the spring when soil temperatures rise again.[9] Within 4–6 weeks of breaking hibernation, the larvae will pupate. Most of the beetle's life is spent as a larva, with only 30–45 days spent as an imago. Adults feed on leaf material above ground, using pheromones to attract other beetles and overwhelm plants, skeletonizing leaves from the top of the plant downward. The aggregation of beetles will alternate daily between mating, feeding, and ovipositing. An adult female may lay as many as 40–60 ova in her lifetime.[9]

A typical cluster of Japanese beetle eggs

Throughout the majority of the Japanese beetle's range, its lifecycle takes one full year, however in the extreme northern parts of its range, as well as high altitude zones as found in its native Japan, development may take two years.[10]

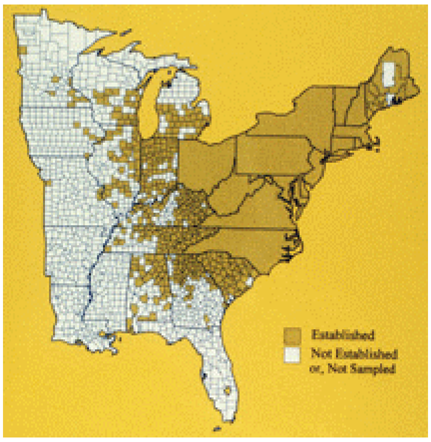
Control

Owing to its destructive nature, traps have been invented specifically to target Japanese beetles. These comprise a pair of crossed walls with a bag or plastic container underneath, and are baited with floral scent, pheromone, or both. However, studies conducted at the University of Kentucky and Eastern Illinois University suggest beetles attracted to traps frequently do not end up in the traps, but alight on plants in the vicinity, thus causing more damage along the flight path of the beetles and near the trap than may have occurred if the trap were not present.[11][12]

A Japanese beetle pupa shortly after moulting

During the larval stage, the Japanese beetle lives in lawns and other grasslands, where it eats the roots of grasses. During that stage, it is susceptible to a fatal disease called milky spore disease, caused by a bacterium called milky spore, *Paenibacillus* (formerly *Bacillus*) *popilliae.* The USDA developed this biological control and it is commercially available in powder form for application to lawn areas. Standard applications (low density across a broad area) take from one to five years to establish maximal protection against larval survival (depending on climate), expanding through the soil through repeated rounds of infection.

On field crops such as squash, floating row covers can be used to exclude the beetles, but this may necessitate hand pollination of flowers. Kaolin sprays can also be used as barriers.



Map showing the parts of the US infested by Japanese beetles, as of November 2006: They were present in many more sites as of July 2012.

Research performed by many US extension service branches has shown pheromone traps attract more beetles than they catch.[13][14] Traps are most effective when spread out over an entire community, and downwind and at the borders (i.e., as far away as possible, particularly upwind), of managed property containing plants being protected. Natural repellents include catnip, chives, garlic, and tansy,[15] as well as the remains of dead beetles, but these methods have limited effectiveness.[16] Additionally, when present in small numbers, the beetles may be manually controlled using a soap-water spray mixture, shaking a plant in the morning hours and disposing of the fallen beetles,[14] or simply picking them off attractions such as rose flowers, since the presence of beetles attracts more beetles to that plant.[16]

Egg of biocontrol, tachinid fly *Istocheta aldrichi*, introduced from Japan

Several insect predators and parasitoids have been introduced to the United States for biocontrol. Two of them, *Istocheta aldrichi* and *Tiphia vernalis*, are well established with significant rates of parasitism.

Hostplants

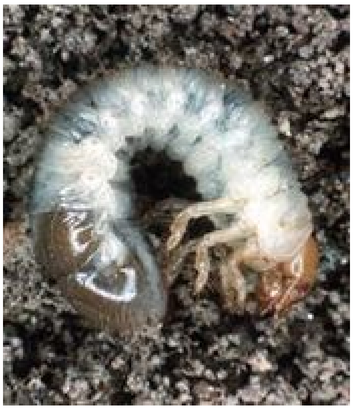
While the larvae of Japanese beetles feed on the roots of many genera of grasses, the adults consume the leaves of a much wider range of hosts, including these common crops:[4] bean, strawberry, tomato, pepper, grape, hop, rose, cherry, plum, pear, peach, raspberry, blackberry, corn, pea, okra, and blueberry.

List of adult beetle hostplant genera

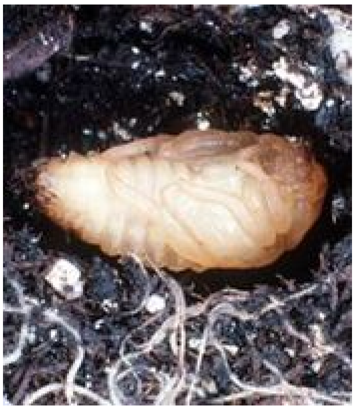
- *Abelmoschus*
- *Acer* (maple)
- *Aesculus* (horse chestnut)
- *Alcea*
- *Aronia*
- *Asimina* (pawpaw)
- *Asparagus*
- *Aster*
- *Buddleja*
- *Calluna*
- *Caladium*
- *Canna*
- *Cannabis sativa*
- *Chaenomeles*
- *Castanea* (sweet chestnut)
- *Cirsium* (thistle)
- *Cosmos*
- *Dahlia*
- *Daucus* (carrot)
- *Dendranthema*
- *Digitalis*
- *Dolichos*
- *Echinacea* (coneflower)
- *Hemerocallis*
- *Heuchera*
- *Hibiscus*
- *Humulus* (hop)
- *Hydrangea*
- *Ilex* (holly)
- *Impatiens*

- *Ipomoea* (morning glory)
- *Iris*
- *Juglans* (walnut)
- *Lagerstroemia*
- *Liatris*
- *Ligustrum* (privet)
- *Malus* (apple, crabapple)
- *Malva* (mallow)
- *Mentha* (mint)
- *Myrica*
- *Ocimum* (basil)
- *Oenothera* (evening primrose)
- *Parthenocissus*
- *Phaseolus*
- *Phlox*
- *Physocarpus*
- *Pistacia*
- *Platanus* (plane)
- *Polygonum* (Japanese knotweed)
- *Populus* (poplar)
- *Prunus* (plum, peach)
- *Quercus* (oak)
- *Ribes* (gooseberry, currants, etc.)
- *Rheum*
- *Rhododendron*
- *Rosa* (rose)
- *Rubus* (raspberry, blackberry, etc.)
- *Salix* (willows)
- *Sambucus* (elder)
- *Sassafras*
- *Solanum* (nightshades, including potato, tomato, eggplant)
- *Spinacia* (spinach)
- *Syringa* (lilac)
- *Thuja* (arborvitae)
- *Tilia* (basswood, linden, UK: lime)
- *Toxicodendron* (poison oak, poison ivy, sumac)
- *Ulmus* (elm)
- *Vaccinium* (blueberry)
- *Viburnum*
- *Vitis* (grape)
- *Weigelia*
- *Wisteria*
- *Zea*
- *Zinnia*

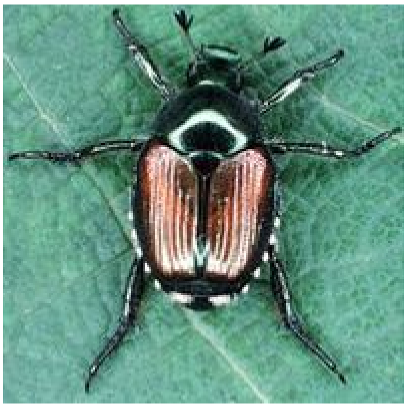
Gallery



Japanese beetle larva (grub)



Japanese beetle pupa



Japanese beetle adult

Adult Japanese beetles feeding on peach tree

Mating, Ottawa, Ontario, Canada

Feeding, Ottawa

Japanese beetle feeding on calla lily, Ottawa, Ontario, Canada

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External links

- Japanese beetle (http://entomology.ifas.ufl.edu/creatures/orn/beetles/japanese_beetle.htm) on the UF/IFAS Featured Creatures Web site
- Japanese Beetle (http://www.inspection.gc.ca/english/plaveg/pestrava/popjap/popjape.shtml), Canadian Food Inspection Agency
- Organic methods of Japanese Beetle Control (http://www.bluehorizonfarm.com/organic-gardening/japanese-beetles.html)
- Species Profile - Japanese Beetle (*Popillia japonica*) (https://www.invasivespeciesinfo.gov/profile/japanese-beetle), National Invasive Species Information Center, United States National Agricultural Library.

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Aphid

Aphids are small sap-sucking insects and members of the superfamily **Aphidoidea**. Common names include **greenfly** and **blackfly**,[a] although individuals within a species can vary widely in colour. The group includes the fluffy white woolly aphids. A typical life cycle involves flightless females giving living birth to female nymphs without the involvement of males. Maturing rapidly, females breed profusely so that the number of these insects multiplies quickly. Winged females may develop later in the season, allowing the insects to colonise new plants. In temperate regions, a phase of sexual reproduction occurs in the autumn, with the insects often overwintering as eggs.

The life cycle of some species involves an alternation between two species of host plants, for example between an annual crop and a woody plant. Some species feed on only one type of plant, while others are generalists, colonising many plant groups. About 5,000 species of aphid have been described, all included in the family Aphididae. Around 400 of these are found on food and fibre crops, and many are serious pests of agriculture and forestry, as well as an annoyance for gardeners. So-called dairying ants have a mutualistic relationship with aphids, tending them for their honeydew, and protecting them from predators.

Aphids are among the most destructive insect pests on cultivated plants in temperate regions. In addition to weakening the plant by sucking sap, they act as vectors for plant viruses and disfigure ornamental plants with deposits of honeydew and the subsequent growth of sooty moulds. Because of their ability to rapidly increase in numbers by asexual reproduction, they are a highly successful group of organisms from an ecological standpoint.[1]

Control of aphids is not easy. Insecticides do not always produce reliable results, given resistance to several classes of insecticide and the fact that aphids often feed on the undersides of leaves. On a garden scale, water jets and soap sprays are quite effective. Natural enemies include predatory ladybugs, hoverfly larvae, parasitic wasps, aphid midge larvae, crab spiders, lacewing larvae, and entomopathogenic fungi. An integrated pest management strategy using biological pest control can work, but is difficult to achieve except in enclosed environments such as glasshouses.

Aphids

Temporal range: Permian–present

PreЄ Є O S D C P T J K PgN

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Hemiptera
Suborder:	Sternorrhyncha
Infraorder:	Aphidomorpha
Superfamily:	Aphidoidea Geoffroy, 1762

Families

- Aphididae Latreille, 1802
- †Bajsaphididae Homan, Zyla & Wegierek, 2015
- †Canadaphididae Richards, 1966
- †Cretamyzidae Heie, 1992
- †Drepanochaitophoridae Zhang & Hong, 1999
- †Oviparosiphidae Shaposhnikov, 1979
- †Parvaverrucosidae Poinar & Brown, 2006

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- †Sinaphididae Zhang, Zhang, Hou & Ma, 1989
- *incertae sedis*
    - †*Palaeoforda tajmyrensis* Kononova, 1977
    - †*Penaphis* Lin, 1980
    - †*Plioaphis subhercynica* Heie, 1968
    - †*Sbenaphis* Scudder, 1890
    - †*Sunaphis* Hong & Wang, 1990
    - †*Xilutiancallis* Wang, 1991
    - †*Yueaphis* Wang, 1993

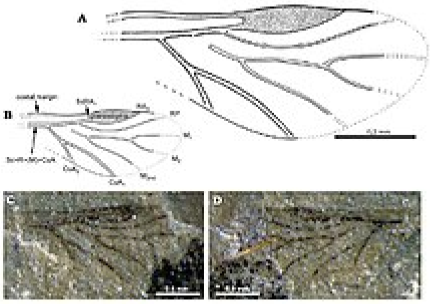
Distribution

Aphids are distributed worldwide, but are most common in temperate zones. In contrast to many taxa, aphid species diversity is much lower in the tropics than in the temperate zones.[2] They can migrate great distances, mainly through passive dispersal by winds. Winged aphids may also rise up in the day as high as 600 m where they are transported by strong winds.[3][4] For example, the currant-lettuce aphid, *Nasonovia ribisnigri*, is believed to have spread from New Zealand to Tasmania around 2004 through easterly winds.[5] Aphids have also been spread by human transportation of infested plant materials, making some species nearly cosmopolitan in their distribution.[6]

Evolution

Fossil history

Aphids, and the closely related adelgids and phylloxerans, probably evolved from a common ancestor some 280 million years ago, in the Early Permian period.[8] They probably fed on plants like Cordaitales or Cycadophyta. With their soft bodies, aphids do not fossilize well, and the oldest known fossil is of the species *Triassoaphis cubitus* from the Triassic.[9] They do however sometimes get stuck in plant exudates which solidify into amber. In 1967, when Professor Ole Heie wrote his monograph *Studies on Fossil Aphids*, about sixty species have been described from the Triassic, Jurassic, Cretaceous and mostly the Tertiary periods, with Baltic amber contributing another forty species.[10] The total number of species was small, but increased considerably with the appearance of the angiosperms 160 million years ago, as this allowed aphids to specialise, the speciation of aphids going hand-in-hand with the diversification of flowering plants. The earliest aphids were probably polyphagous, with monophagy developing later.[11] It has been hypothesized that the ancestors of the Adelgidae lived on conifers while those of the Aphididae fed on the sap of Podocarpaceae or Araucariaceae that survived extinctions in the late Cretaceous. Organs like the cornicles did not appear until the Cretaceous period.[8][12] One study alternatively suggests that ancestral aphids may have lived on angiosperm bark and that feeding on leaves may be a derived trait. The Lachninae have long mouth parts that are suitable for living on bark and it has been suggested that the mid-Cretaceous ancestor fed on the bark of angiosperm trees, switching to leaves of conifer hosts in the late Cretaceous.[13] The Phylloxeridae may well be the oldest family still extant, but their fossil record is limited to the Lower Miocene *Palaeophylloxera*.[14]



Forewing of the early Middle Triassic (early Anisian) aphid *Vosegus triassicus*[7]

Taxonomy

An aphid fossilised in Baltic amber (Eocene)

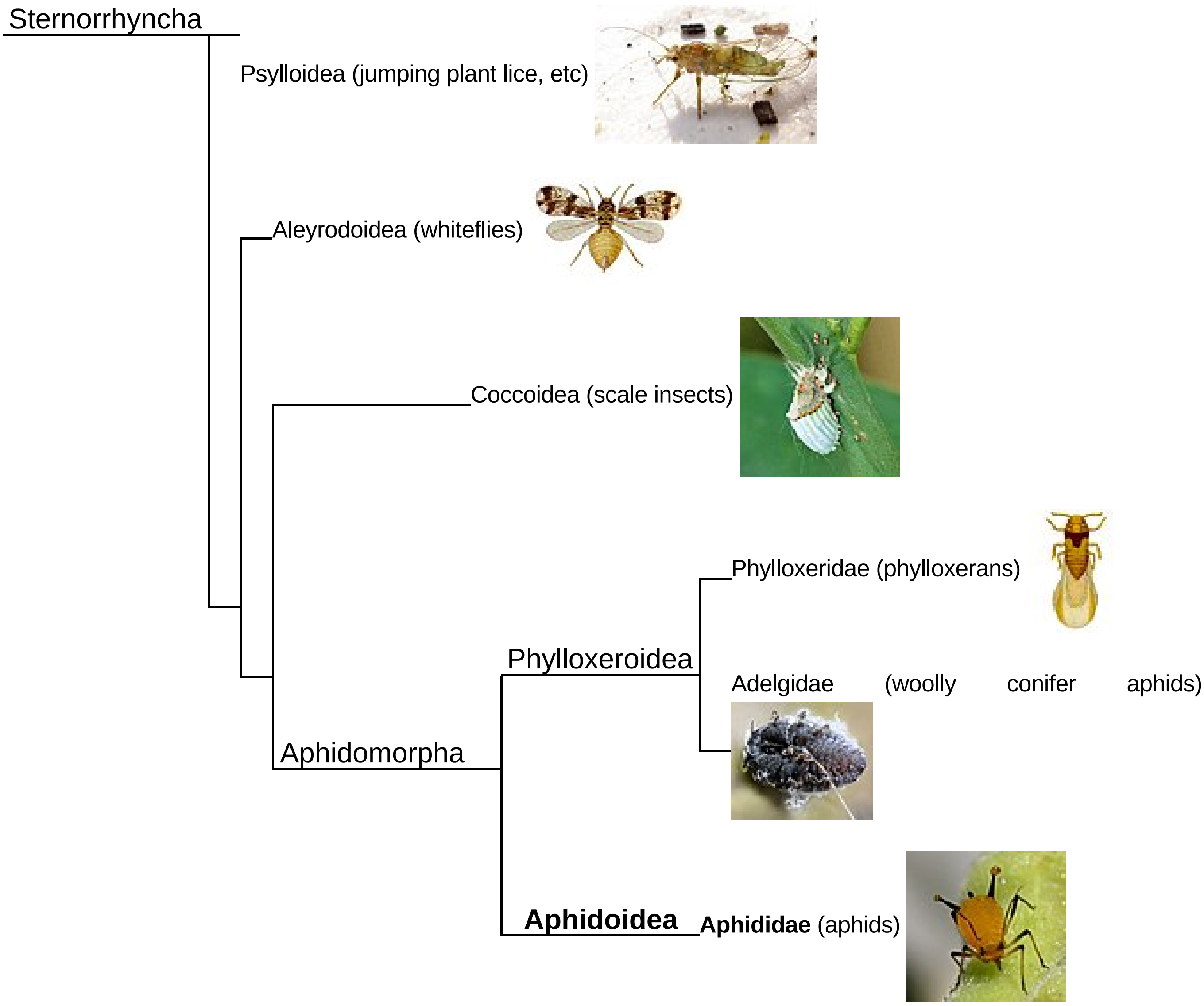
Late 20th-century reclassification within the Hemiptera reduced the old taxon "Homoptera" to two suborders: Sternorrhyncha (aphids, whiteflies, scales, psyllids, etc.) and Auchenorrhyncha (cicadas, leafhoppers, treehoppers, planthoppers, etc.) with the suborder Heteroptera containing a large group of insects known as the true bugs. The infraorder Aphidomorpha within the Sternorrhyncha varies with circumscription with several fossil groups being especially difficult to place but includes the Adelgoidea, the Aphidoidea and the Phylloxeroidea.[15] Some authors use a single superfamily Aphidoidea within which the Phylloxeridae and Adelgidae are also included while others have Aphidoidea with a sister superfamily Phylloxeroidea within which the Adelgidae and Phylloxeridae are placed.[16] Early 21st-century reclassifications substantially rearranged the families within Aphidoidea: some old families were reduced to subfamily rank (*e.g.*, Eriosomatidae), and many old subfamilies were elevated to family rank. The most recent authoritative classifications have three superfamilies Adelgoidea, Phylloxeroidea and Aphidoidea. The Aphidoidea includes a single large family Aphididae that includes all the ~5000[2] extant species.[17]

Phylogeny

External

Aphids, adelgids, and phylloxerids are very closely related, and are all within the suborder Sternorrhyncha, the plant-sucking bugs. They are either placed in the insect superfamily Aphidoidea[18] or into the superfamily Phylloxeroidea which contains the family Adelgidae and the family Phylloxeridae.[11] Like aphids, phylloxera feed on the roots, leaves, and shoots of grape plants, but unlike aphids, do not produce honeydew or cornicle secretions.[19] Phylloxera (*Daktulosphaira vitifoliae*) are insects which caused the Great French Wine Blight that devastated European viticulture in the 19th century. Similarly, adelgids or woolly conifer aphids, also feed on plant phloem and are sometimes described as aphids, but are more properly classified as aphid-like insects, because they have no cauda or cornicles.[20]

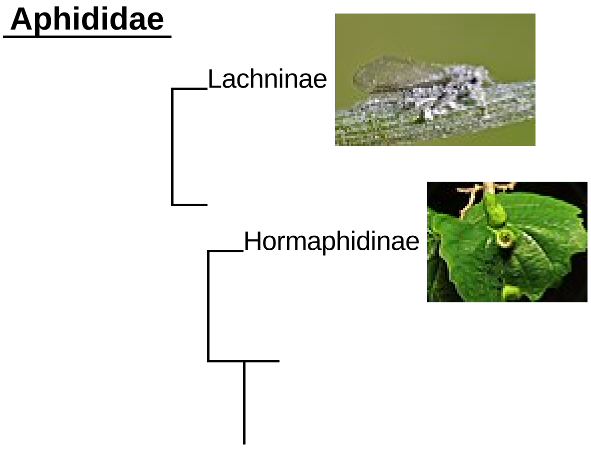
The treatment of the groups especially with respect to fossil groups varies greatly due to difficulties in resolving relationships. Most modern treatments include the three superfamilies, the Adelogidea, the Aphidoidea and the Phylloxeroidea within the infraorder Aphidomorpha along with several fossil groups[21] but other treatments have the Aphidomorpha containing the Aphidoidea with the families Aphididae, Phylloxeridae and Adelgidae; or the Aphidomorpha with two superfamilies, Aphidoidea and Phylloxeroidea, the latter containing the Phylloxeridae and the Adelgidae. The phylogenetic tree of the Sternorrhyncha is inferred from analysis of small subunit (18S) ribosomal RNA.[22]

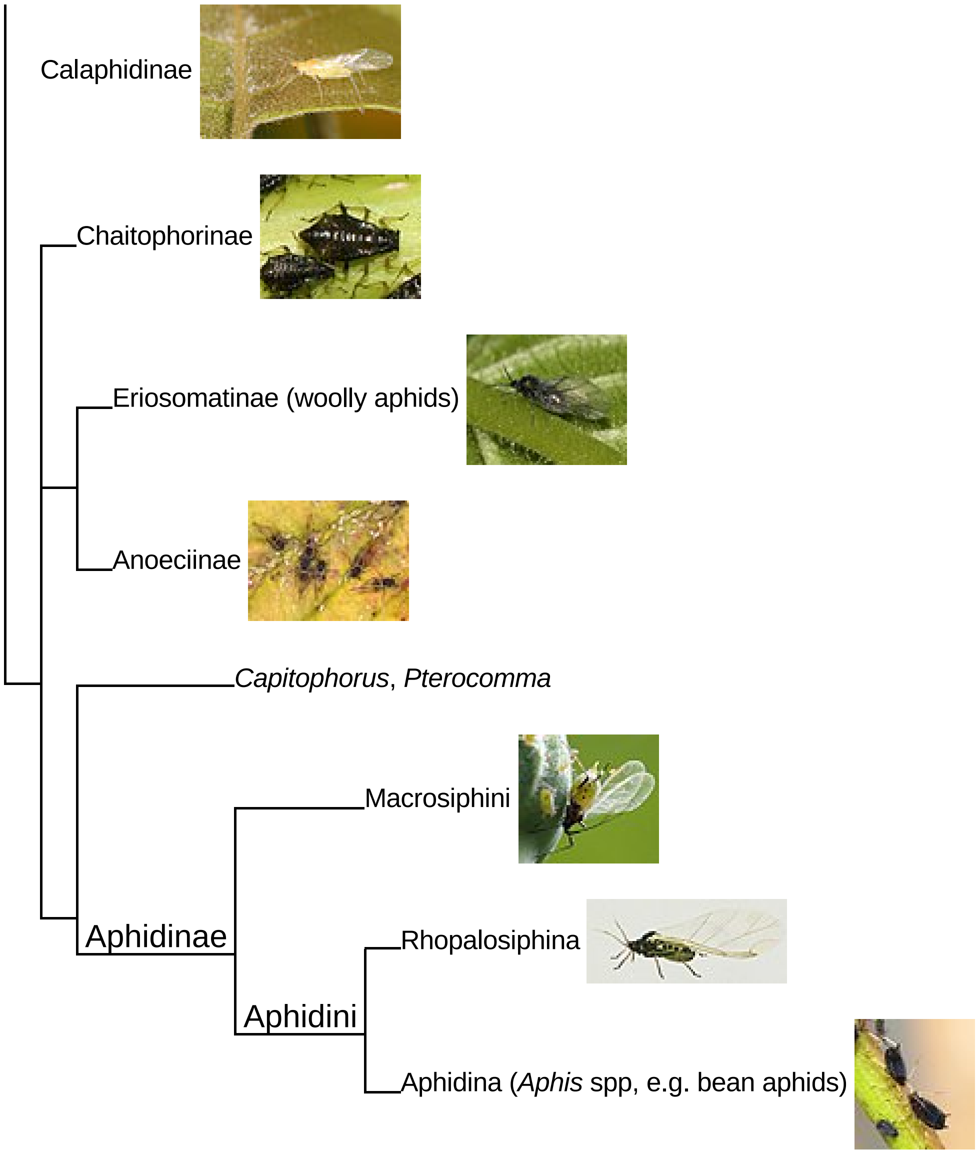

Sternorrhyncha
Psylloidea (jumping plant lice, etc)
Aleyrodoidea (whiteflies)
Coccoidea (scale insects)
Phylloxeridae (phylloxerans)
Phylloxeroidea
Adelgidae (woolly conifer aphids)
Aphidomorpha
Aphidoidea
Aphididae (aphids)

Internal

The phylogenetic tree, based on Papasotiropoulos 2013 and Kim 2011, with additions from Ortiz-Rivas and Martinez-Torres 2009, shows the internal phylogeny of the Aphididae.[23][24][25]

It has been suggested that the phylogeny of the aphid groups might be revealed by examining the phylogeny of their bacterial endosymbionts, especially the obligate endosymbiont *Buchnera*. The results depend on the assumption that the symbionts are strictly transmitted vertically through the generations. This assumption is well supported by the evidence, and several phylogenetic relationships have been suggested on the basis of endosymbiont studies.[26][27][28]

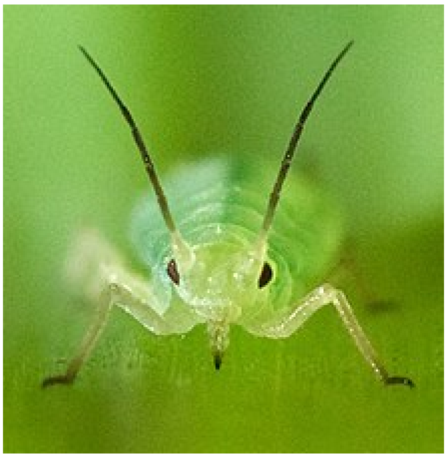



Calaphidinae
Chaitophorinae
Eriosomatinae (woolly aphids)
Anoeciinae
Capitophorus, *Pterocomma*
Macrosiphini
Aphidinae
Rhopalosiphina
Aphidini
Aphidina (*Aphis* spp, e.g. bean aphids)

Anatomy

Most aphids have soft bodies, which may be green, black, brown, pink, or almost colorless. Aphids have antennae with two short, broad basal segments and up to four slender terminal segments. They have a pair of compound eyes, with an ocular tubercle behind and above each eye, made up of three lenses (called triommatidia).[11] They feed on sap using sucking mouthparts called stylets, enclosed in a sheath called a rostrum, which is formed from modifications of the mandible and maxilla of the insect mouthparts.[29]

They have long, thin legs with two-jointed, two-clawed tarsi. The majority of aphids are wingless, but winged forms are produced at certain times of year in many species. Most aphids have a pair of cornicles (siphunculi), abdominal tubes on the dorsal surface of their fifth abdominal segment, through which they exude droplets of a quick-hardening defensive fluid[29] containing triacylglycerols, called cornicle wax. Other defensive compounds can also be produced by some species.[20] Aphids have a tail-like protrusion called a cauda above their rectal apertures.[11][30]


Front view of wheat aphid, *Schizaphis graminum*, showing the piercing-sucking mouthparts

When host plant quality becomes poor or conditions become crowded, some aphid species produce winged offspring (alates) that can disperse to other food sources. The mouthparts or eyes can be small or missing in some species and forms.[20]

Diet

Many aphid species are monophagous (that is, they feed on only one plant species). Others, like the green peach aphid feed on hundreds of plant species across many families. About 10% of species feed on different plants at different times of year.[31]

A new host plant is chosen by a winged adult by using visual cues, followed by olfaction using the antennae; if the plant smells right, the next action is probing the surface upon landing. The stylus is inserted and saliva secreted, the sap is sampled, the xylem may be tasted and finally the phloem is tested. Aphid saliva may inhibit phloem-sealing mechanisms and has pectinases that ease penetration.[32] Non-host plants can be rejected at any stage of the probe, but the transfer of viruses occurs early in the investigation process, at the time of the introduction of the saliva, so non-host plants can become infected.[31]

Aphids usually feed passively on sap of phloem vessels in plants, as do many of other hemipterans such as scale insects and cicadas. Once a phloem vessel is punctured, the sap, which is under pressure, is forced into the aphid's food canal. Occasionally, aphids also ingest xylem sap, which is a more dilute diet than phloem sap as the concentrations of sugars and amino acids are 1% of those in the phloem.[33][34] Xylem sap is under negative hydrostatic pressure and requires active sucking, suggesting an important role in aphid physiology.[35] As xylem sap ingestion has been observed following a dehydration period, aphids are thought to consume xylem sap to replenish their water balance; the consumption of the dilute sap of xylem permitting aphids to rehydrate.[36] However, recent data showed aphids consume more xylem sap than expected and they notably do so when they are not dehydrated and when their fecundity decreases. This suggests aphids, and potentially, all the phloem-sap feeding species of the order Hemiptera, consume xylem sap for reasons other than replenishing water balance.[37] Although aphids passively take in phloem sap, which is under pressure, they can also draw fluid at negative or atmospheric pressure using the cibarial-pharyngeal pump mechanism present in their head.[38]

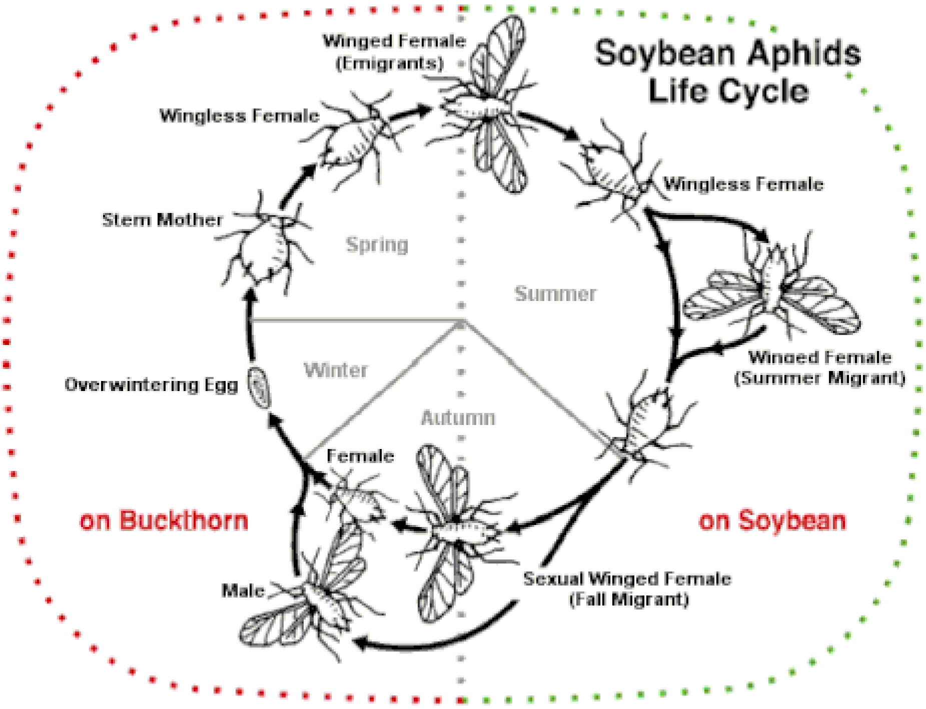
Xylem sap consumption may be related to osmoregulation.[37] High osmotic pressure in the stomach, caused by high sucrose concentration, can lead to water transfer from the hemolymph to the stomach, thus resulting in hyperosmotic stress and eventually to the death of the insect. Aphids avoid this fate by osmoregulating through several processes. Sucrose concentration is directly reduced by assimilating sucrose toward metabolism and by synthesizing oligosaccharides from several sucrose molecules, thus reducing the solute concentration and consequently the osmotic pressure.[39][40] Oligosaccharides are then excreted through honeydew, explaining its high sugar concentrations, which can then be used by other animals such as ants. Furthermore, water is transferred from the hindgut, where osmotic pressure has already been reduced, to the stomach to dilute stomach content.[41] Eventually, aphids consume xylem sap to dilute the stomach osmotic pressure.[37] All these processes function synergetically, and enable aphids to feed on high-sucrose-concentration plant sap, as well as to adapt to varying sucrose concentrations.[37]

Plant sap is an unbalanced diet for aphids, as it lacks essential amino acids, which aphids, like all animals, cannot synthesise, and possesses a high osmotic pressure due to its high sucrose concentration.[34][42] Essential amino acids are provided to aphids by bacterial endosymbionts, harboured in special cells, bacteriocytes.[43] These symbionts recycle glutamate, a metabolic waste of their host, into essential amino acids.[44][45]

Carotenoids and photoheterotrophy

Some species of aphids have acquired the ability to synthesise red carotenoids by horizontal gene transfer from fungi.[46] They are the only animals other than two-spotted spider mites with this capability.[47] Using their carotenoids, aphids may well be able to absorb solar energy and convert it to a form that their cells can use, ATP. This is the only known example of photoheterotrophy in animals. The carotene pigments in aphids form a layer close to the surface of the cuticle, ideally placed to absorb sunlight. The excited carotenoids seem to reduce NAD to NADH which is oxidized in the mitochondria for energy.[48]

Reproduction


Soybean Aphids Life Cycle
Winged Female (Emigrants)
Wingless Female
Stem Mother
Spring
Summer
Wingless Female
Winged Female (Summer Migrant)
Overwintering Egg
Winter
Autumn
Female
on Buckthorn
on Soybean
Male
Sexual Winged Female (Fall Migrant)

Soybean aphid alternates between hosts and between asexual and sexual reproduction.[49]

The simplest reproductive strategy is for an aphid to have a single host all year round. On this it may alternate between sexual and asexual generations (holocyclic) or alternatively, all young may be produced by parthenogenesis, eggs never being laid (anholocyclic). Some species can have both holocyclic and anholocyclic populations under different circumstances but no known aphid species reproduce solely by sexual means.[50] The alternation of sexual and asexual generations may have evolved repeatedly.[51]

However, aphid reproduction is often more complex than this and involves migration between different host plants. In about 10% of species, there is an alternation between woody (primary hosts) on which the aphids overwinter and herbaceous (secondary) host plants, where they reproduce abundantly in the summer.[20][50] A few species can produce a soldier caste, other species show extensive polyphenism under different environmental conditions and some can control the sex ratio of their offspring depending on external factors.[52]

When a typical sophisticated reproductive strategy is used, only females are present in the population at the beginning of the seasonal cycle (although a few species of aphids have been found to have both male and female sexes at this time). The overwintering eggs that hatch in the spring result in females, called fundatrices (stem mothers). Reproduction typically does not involve males (parthenogenesis) and results in live birth (viviparity).[53] The live young are produced by pseudoplacental viviparity, which is the development of eggs, deficient in yolk, the embryos fed by a tissue acting as a placenta. The young emerge from the mother soon after hatching.[54]

Eggs are parthenogenetically produced without meiosis[55][53] and the offspring are clonal to their mother, so they are all female (thelytoky).[11][54] The embryos develop within the mothers' ovarioles, which then give birth to live (already hatched) first-instar female nymphs. As the eggs begin to develop immediately after ovulation, an adult female can house developing female nymphs which already have parthenogenetically developing embryos inside them. This telescoping of generations enables aphids to increase in number with great rapidity. The offspring resemble their parent in every way except size. Thus, a female's diet can affect the body size and birth rate of more than two generations (daughters and granddaughters).[11][56][57]

This process repeats itself throughout the summer, producing multiple generations that typically live 20 to 40 days. For example, some species of cabbage aphids (like *Brevicoryne brassicae*) can produce up to 41 generations of females in a season. Thus, one female hatched in spring can theoretically produce billions of descendants, were they all to survive.[58]

Aphid giving birth to live young: populations are often entirely female.

In autumn, aphids reproduce sexually and lay eggs. Environmental factors such as change in photoperiod and temperature, or perhaps a lower food quantity or quality, causes females to parthenogenetically produce sexual females and males.[55] The males are genetically identical to their mothers except that, with the aphids' X0 sex-determination system, they have one fewer sex chromosome.[55] These sexual aphids may lack wings or even mouthparts.[20] Sexual females and males mate, and females lay eggs that develop outside the mother. The eggs survive the winter and hatch into winged (alate) or wingless females the following spring. This occurs in, for example, the life cycle of the rose aphid (*Macrosiphum rosae*), which may be considered typical of the family. However, in warm environments, such as in the tropics or in a greenhouse, aphids may go on reproducing asexually for many years.[29]

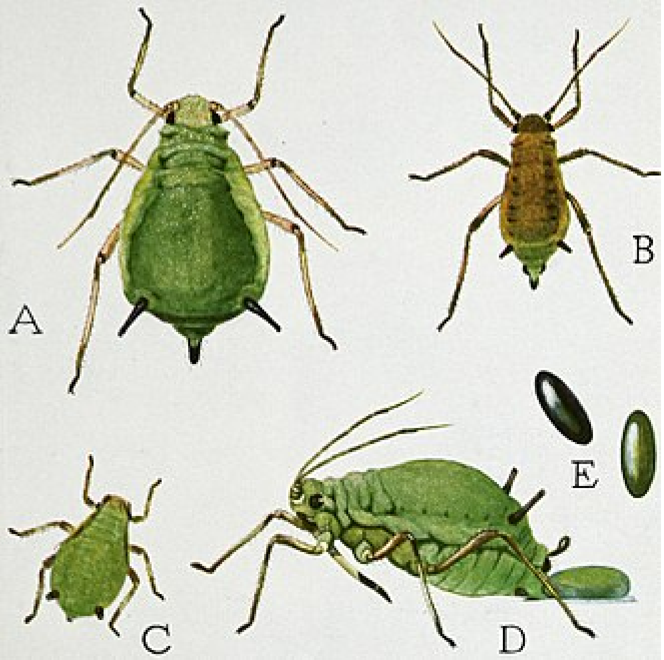
Aphids reproducing asexually by parthenogenesis can have genetically identical winged and non-winged female progeny. Control is complex; some aphids alternate during their life-cycles between genetic control (polymorphism) and environmental control (polyphenism) of production of winged or wingless forms.[59] Winged progeny tend to be produced more abundantly under unfavorable or stressful conditions. Some species produce winged progeny in response to low food quality or quantity. e.g. when a host plant is starting to senesce.[60] The winged females migrate to start new colonies on a new host plant. For example, the apple aphid (*Aphis pomi*), after producing many generations of wingless females gives rise to winged forms that fly to other branches or trees of its typical food plant.[61] Aphids that are attacked by ladybugs, lacewings, parasitoid wasps, or other predators can change the dynamics of their progeny production. When aphids are attacked by these predators, alarm pheromones, in particular beta-farnesene, are released from the cornicles. These alarm pheromones cause several behavioral modifications that, depending on the aphid species, can include walking away and dropping off the host plant. Additionally, alarm pheromone perception can induce the aphids to produce winged progeny that can leave the host plant in search of a safer feeding site.[62] Viral infections, which can be extremely harmful to aphids, can also lead to the production of winged offspring.[63] For example, *Densovirus* infection has a negative impact on rosy apple aphid (*Dysaphis plantaginea (https://influentialpoints.com/Gallery/Dysaphis_plantaginea_Rosy_apple_aphid.htm)*) reproduction, but contributes to the development of aphids with wings, which can transmit the virus more easily to new host plans.[64] Additionally, symbiotic bacteria that live inside of the aphids can also alter aphid reproductive strategies based on the exposure to environmental stressors.[65]

In the autumn, host-alternating (heteroecious) aphid species produce a special winged generation that flies to different host plants for the sexual part of the life cycle. Flightless female and male sexual forms are produced and lay eggs .[66] Some species such as *Aphis fabae* (blackfly of beans), *Metopolophium dirhodum* (rose-grain aphid), *Myzus persicae* (peach-potato aphid), and *Rhopalosiphum padi* (bird cherry-oat aphid) and *Aphis glycines* (soybean aphid)[49] are serious pests. They overwinter on tree or bush primary hosts; in summer, they migrate to their secondary host on a herbaceous plant, often a crop, then the gynoparae return to the tree in autumn. Another example is the soybean aphid (*Aphis glycines*). As fall approaches, the soybean plants begin to senesce from the bottom upwards. The aphids are forced upwards and start to produce winged forms, first females and later males, which fly off to the primary host, buckthorn. Here they mate and overwinter as eggs.[49]

Ecology

Ant mutualism

Some species of ants farm aphids, protecting them on the plants where they are feeding, and consuming the honeydew the aphids release from the terminations of their alimentary canals. This is a mutualistic relationship, with these dairying ants milking the aphids by stroking them with their antennae.[b][67] Although mutualistic, the feeding behaviour of aphids is altered by ant attendance. Aphids attended by ants tend to increase the production of honeydew in smaller drops with a greater concentration of amino acids.[68]



The life stages of the green apple aphid (*Aphis pomi*). Drawing by Robert Evans Snodgrass, 1930

Some farming ant species gather and store the aphid eggs in their nests over the winter. In the spring, the ants carry the newly hatched aphids back to the plants. Some species of dairying ants (such as the European yellow meadow ant, *Lasius flavus*)[69] manage large herds of aphids that feed on roots of plants in the ant colony. Queens leaving to start a new colony take an aphid egg to found a new herd of underground aphids in the new colony. These farming ants protect the aphids by fighting off aphid predators.[67]

Ants tending aphids

An ant guards its aphids

Ant extracting honeydew from an aphid

An interesting variation in ant–aphid relationships involves lycaenid butterflies and *Myrmica* ants. For example, *Niphanda fusca* butterflies lay eggs on plants where ants tend herds of aphids. The eggs hatch as caterpillars which feed on the aphids. The ants do not defend the aphids from the caterpillars, since the caterpillars produce a pheromone which deceives the ants into treating them like ants, and carrying the caterpillars into their nest. Once there, the ants feed the caterpillars, which in return produce honeydew for the ants. When the caterpillars reach full size, they crawl to the colony entrance and form cocoons. After two weeks, the adult butterflies emerge and take flight. At this point, the ants attack the butterflies, but the butterflies have a sticky wool-like substance on their wings that disables the ants' jaws, allowing the butterflies to fly away without being harmed.[70] Some bees in coniferous forests collect aphid honeydew to make forest honey.[29]

Another ant-mimicking gall aphid, *Paracletus cimiciformis* (Eriosomatinae), has evolved a complex double strategy involving two morphs of the same clone and *Tetramorium* ants. Aphids of the round morph cause the ants to farm them, as with many other aphids. The flat morph aphids are aggressive mimics with a "wolf in sheep's clothing" strategy: they have hydrocarbons in their cuticle that mimic those of the ants, and the ants carry them into the brood chamber of the ants' nest and raise them like ant larvae. Once there, the flat morph aphids behave as predators, drinking the body fluids of ant larvae.[71]

Bacterial endosymbiosis

Endosymbiosis with micro-organisms is common in insects, with more than 10% of insect species relying on intracellular bacteria for their development and survival.[72] Aphids harbour a vertically transmitted (from parent to its offspring) obligate symbiosis with *Buchnera aphidicola*, the primary symbiont, inside specialised cells, the bacteriocytes.[73] Five of the bacteria genes have been transferred to the aphid nucleus.[74] The original contamination occurred in a common ancestor 280 to 160 million years ago and enabled aphids to exploit a new ecological niche, feeding on phloem-sap of vascular plants. *B. aphidicola* provides its host with essential amino acids, which are present in low concentrations in plant sap. The stable intracellular conditions, as well as the bottleneck effect experienced during the transmission of a few bacteria from the mother to each nymph, increase the probability of transmission of mutations and gene deletions.[75][76] As a result, the size of the *B. aphidicola* genome is greatly reduced, compared to its putative ancestor.[77] Despite the apparent loss of transcription factors in the reduced genome, gene expression is highly regulated, as shown by the ten-fold variation in expression levels between different genes under normal conditions.[78] *Buchnera aphidicola* gene transcription, although not well understood, is thought to be regulated by a small number of global transcriptional regulators and/or through nutrient supplies from the aphid host.[79]

Some aphid colonies also harbour secondary or facultative (optional extra) bacterial symbionts. These are vertically transmitted, and sometimes also horizontally (from one lineage to another and possibly from one species to another).[80][81] So far, the role of only some of the secondary symbionts has been described; *Regiella insecticola* plays a role in defining the host-plant range,[82][83] *Hamiltonella defensa* provides resistance to parasitoids but only when it is in turn infected by the bacteriophage APSE,[84][85] and *Serratia symbiotica* prevents the deleterious effects of heat.[86]

Predators

Aphids are eaten by many bird and insect predators. In a study on a farm in North Carolina, six species of passerine bird consumed nearly a million aphids per day between them, the top predators being the American goldfinch, with aphids forming 83% of its diet, and the vesper sparrow.[87] Insects that attack aphids include the adults and larvae of predatory ladybirds, hoverfly larvae, parasitic wasps, aphid midge larvae, "aphid lions" (the larvae of green lacewings), and arachnids such as crab spiders. Among ladybirds, *Myzia oblongoguttata* is a dietary specialist which only feeds on conifer aphids, whereas *Adalia bipunctata* and *Coccinella septempunctata* are generalists, feeding on large numbers of species. The eggs are laid in batches, each female laying several hundred. Female hoverflies lay several thousand eggs. The adults feed on pollen and nectar but the larvae feed voraciously on aphids; *Eupeodes corollae* adjusts the number of eggs laid to the size of the aphid colony.[88]

Aphids are often infected by bacteria, viruses, and fungi. They are affected by the weather, such as precipitation,[89] temperature[90] and wind.[91] Fungi that attack aphids include *Neozygites fresenii*, *Entomophthora*, *Beauveria bassiana*, *Metarhizium anisopliae*, and entomopathogenic fungi such as *Lecanicillium lecanii*. Aphids brush against the microscopic spores. These stick to the aphid, germinate, and penetrate the aphid's skin. The fungus grows in the aphid's hemolymph. After about three days, the aphid dies and the fungus releases more spores into the air. Infected aphids are covered with a woolly mass that progressively grows thicker until the aphid is obscured. Often, the visible fungus is not the one that killed the aphid, but a secondary infection.[89]

Aphids can be easily killed by unfavourable weather, such as late spring freezes.[92] Excessive heat kills the symbiotic bacteria that some aphids depend on, which makes the aphids infertile.[93] Rain prevents winged aphids from dispersing, and knocks aphids off plants and thus kills them from the impact or by starvation,[89][94][95] but cannot be relied on for aphid control.[96]

Anti-predator defences

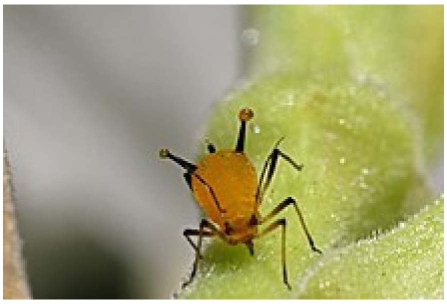
Predators eating aphids

Ladybird larva

Hoverfly larva

The ladybird beetle *Propylea quatuordecimpunctata*

Most aphids have little protection from predators. Some species interact with plant tissues forming a gall, an abnormal swelling of plant tissue. Aphids can live inside the gall, which provides protection from predators and the elements. A number of galling aphid species are known to produce specialised "soldier" forms, sterile nymphs with defensive features which defend the gall from invasion.[29][97][98] For example, Alexander's horned aphids are a type of soldier aphid that has a hard exoskeleton and pincer-like mouthparts.[70]:144 A woolly aphid, *Colophina clematis*, has first instar "soldier" larvae that protect the aphid colony, killing larvae of ladybirds, hoverflies and the flower bug *Anthocoris nemoralis* by climbing on them and inserting their stylets.[99]



Aphid secreting defensive fluid from the cornicles

Although aphids cannot fly for most of their life cycle, they can escape predators and accidental ingestion by herbivores by dropping off the plant onto the ground.[100] Others species use the soil as a permanent protection, feeding on the vascular systems of roots and remaining underground all their lives. They are often attended by ants, for the honeydew they produce, and are carried from plant to plant by the ants through their tunnels.[87]

Some species of aphid, known as "woolly aphids" (Eriosomatinae), excrete a "fluffy wax coating" for protection.[29] The cabbage aphid, *Brevicoryne brassicae*, sequesters secondary metabolites from its host, stores them and releases chemicals that produce a violent chemical reaction and strong mustard oil smell to repel predators.[101] Peptides produced by aphids, Thaumatins, are thought to provide them with resistance to some fungi.[102]

It was common at one time to suggest that the cornicles were the source of the honeydew, and this was even included in the *Shorter Oxford English Dictionary*[103] and the 2008 edition of the *World Book Encyclopedia*.[104] In fact, honeydew secretions are produced from the anus of the aphid,[105] while cornicles mostly produce defensive chemicals such as waxes. There also is evidence of cornicle wax attracting aphid predators in some cases.[106]

Some clones of *Aphis craccivora* are sufficiently toxic to the invasive and dominant predatory ladybird *Harmonia axyridis* to suppress it locally, favouring other ladybird species; the toxicity is in this case narrowly specific to the dominant predator species.[107]

Parasitoids

Aphids are abundant and widespread, and serve as hosts to a large number of parasitoids, many of them being very small (c. 0.1 inches (2.5 mm) long) parasitoid wasps.[108] One species, *Aphis ruborum*, for example, is host to at least 12 species of parasitoid wasps.[109] Parasitoids have been investigated intensively as biological control agents, and many are used commercially for this purpose.[110]

Plant-aphid interactions

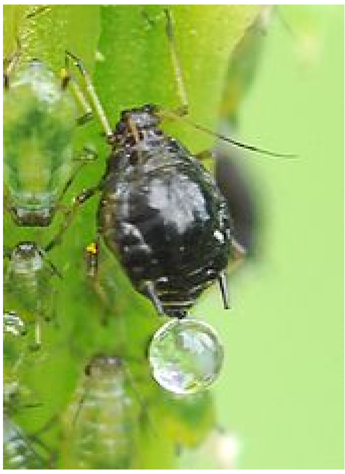
Aphids on plant host

Plants mount local and systemic defences against aphid attack. Young leaves in some plants contain chemicals which discourage attack while the older leaves have lost this resistance, while in other plant species, resistance is acquired by older tissues and the young shoots are vulnerable. Volatile products from interplanted onions have been shown to prevent aphid attack on adjacent potato plants by encouraging the production of terpenoids, a benefit exploited in the traditional practice of companion planting, while plants neighbouring infested plants showed increased root growth at the expense of the extension of aerial parts.[31] The wild potato, *Solanum berthaultii*, produces an aphid alarm pheromone, (E)-β-farnesene, as an allomone, a pheromone to ward off attack; it effectively repels the aphid *Myzus persicae* at a range of up to 3 millimetres.[111] *S. berthaultii* and other wild potato species have a further anti-aphid defence in the form of glandular hairs which, when broken by aphids, discharge a sticky liquid that can immobilise some 30% of the aphids infesting a plant.[112]

Plants exhibiting aphid damage can have a variety of symptoms, such as decreased growth rates, mottled leaves, yellowing, stunted growth, curled leaves, browning, wilting, low yields and death. The removal of sap creates a lack of vigour in the plant, and aphid saliva is toxic to plants. Aphids frequently transmit plant viruses to their hosts, such as to potatoes, cereals, sugarbeets, and citrus plants.[29] The green peach aphid, *Myzus persicae*, is a vector for more than 110 plant viruses. Cotton aphids (*Aphis gossypii*) often infect sugarcane, papaya and peanuts with viruses.[20] In plants which produce the phytoestrogen coumestrol, such as alfalfa, damage by aphids is linked with higher concentrations of coumestrol.[113]

The coating of plants with honeydew can contribute to the spread of fungi which can damage plants.[114][115] Honeydew produced by aphids has been observed to reduce the effectiveness of fungicides as well.[116]

A hypothesis that insect feeding may improve plant fitness was floated in the mid-1970s by Owen and Wiegert. It was felt that the excess honeydew would nourish soil micro-organisms, including nitrogen fixers. In a nitrogen poor environment, this could provide an advantage to an infested plant over an uninfested plant. However, this does not appear to be supported by the observational evidence.[117]


Aphid with honeydew, from the anus not the cornicles

Sociality

Some aphids show some of the traits of eusociality, joining insects such as ants, bees and termites. However, there are differences between these sexual social insects and the clonal aphids, which are all descended from a single female parthenogenetically and share an identical genome. About fifty species of aphid, scattered among the closely related, host-alternating families Pemphigidae and Hormaphididae, have some type of defensive morph. These are gall-creating species, with the colony living and feeding inside a gall that they form in the host's tissues. Among the clonal population of these aphids there may be a number of distinct morphs and this lays the foundation for a possible specialisation of function, in this case, a defensive caste. The soldier morphs are mostly first and second instars with the third instar being involved in *Eriosoma moriokense* and only in *Smythurodes betae* are adult soldiers known. The hind legs of soldiers are clawed, heavily sclerotised and the stylets are robust making it possible to rupture and crush small predators.[118] The larval soldiers are altruistic individuals, unable to advance to breeding adults but acting permanently in the interests of the colony. Another requirement for the development of sociality is provided by the gall, a colonial home to be defended by the soldiers.[119]

The soldiers of gall forming aphids also carry out the job of cleaning the gall. The honeydew secreted by the aphids is coated in a powdery wax to form "liquid marbles"[120] that the soldiers roll out of the gall through small orifices.[98] Aphids that form closed galls use the plant's vascular system for their plumbing: the inner surfaces of the galls are highly absorbent and wastes are absorbed and carried away by the plant.[98]

Interactions with humans

Pest status

About 5000 species of aphid have been described and of these, some 450 species have colonised food and fibre crops. As direct feeders on plant sap, they damage crops and reduce yields, but they have a greater impact by being vectors of plant viruses. The transmission of these viruses depends on the movements of aphids between different parts of a plant, between nearby plants and further afield. In this respect, the probing behaviour of an aphid tasting a host is more damaging than lengthy aphid feeding and reproduction by stay-put individuals. The movement of aphids influences the timing of virus epidemics.[121]

Aphids, especially during large outbreaks, have been known to trigger allergic inhalant reactions in sensitive humans.[122]

Dispersal can be by walking or flight, appetitive dispersal or by migration. Winged aphids are weak fliers, lose their wings after a few days and only fly by day. Dispersal by flight is affected by impact, air currents, gravity, precipitation and other factors, or dispersal may be accidental, caused by movement of plant materials, animals, farm machinery, vehicles or aircraft.[121]

Control

Parasitoid braconid wasp ovipositing in black bean aphid

Insecticide control of aphids is difficult, as they breed rapidly, so even small areas missed may enable the population to recover promptly. Aphids may occupy the undersides of leaves where spray misses them, while systemic insecticides do not move satisfactorily into flower petals. Finally, some aphid species are resistant to common insecticide classes including carbamates, organophosphates, and pyrethroids.[123]

For small backyard infestations, spraying plants thoroughly with a strong water jet every few days may be sufficient protection. An insecticidal soap solution can be an effective household remedy to control aphids, but it only kills aphids on contact and has no residual effect. Soap spray may damage plants, especially at higher concentrations or at temperatures above 32 °C (90 °F); some plant species are sensitive to soap sprays.[110][124][125]

Integrated pest management of various species of aphids can be achieved using biological insecticides based on fungi such as *Lecanicillium lecanii*, *Beauveria bassiana* or *Isaria fumosorosea*.[126] Fungi are the main pathogens of aphids; Entomophthorales can quickly cut aphid numbers in nature.[127]

Aphids may also be controlled by the release of natural enemies, in particular lady beetles and parasitoid wasps. However, since adult lady beetles tend to fly away within 48 hours after release, without laying eggs, repeated applications of large numbers of lady beetles are needed to be effective. For example, one large, heavily infested rose bush may take two applications of 1500 beetles each.[110][128]

The ability to produce allomones such as farnesene to repel and disperse aphids and to attract their predators has been experimentally transferred to transgenic *Arabidopsis thaliana* plants using an Eβf synthase gene in the hope that the approach could protect transgenic crops.[129] Eβ farnesene has however found to be ineffective in crop situations although stabler synthetic forms help improve the effectiveness of control using fungal spores and insecticides through increased uptake caused by movements of aphids.[130]

Green peach aphid, *Myzus persicae*, killed by the fungus *Pandora neoaphidis* (Entomophthorales)

In human culture

Aphids are familiar to farmers and gardeners, mainly as pests. Peter Marren and Richard Mabey record that Gilbert White described an invading "army" of black aphids that arrived in his village of Selborne in August 1774 in "great clouds", covering every plant, while in the unusually hot summer of 1783, White found that honeydew was so abundant as to "deface and destroy the beauties of my garden", though he thought the aphids were consuming rather than producing it.[131]

Infestation of the Chinese sumac (*Rhus chinensis*) by Chinese sumac aphids (*Schlechtendalia chinensis*) can create "Chinese galls" which are valued as a commercial product. As "Galla Chinensis", they are used in traditional Chinese medicine to treat coughs, diarrhoea, night sweats, dysentery and to stop intestinal and uterine bleeding. Chinese galls are also an important source of tannins.[29]

See also

- Aeroplankton
- Economic entomology
- Pineapple gall

Notes

a. The term "black fly" is also used for the Simuliidae, among them the vector of river blindness.

b. Dairying ants also milk mealybugs and other insects.

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Caterpillar

Caterpillar of *Papilio machaon*

Caterpillars /ˈkætərˌpɪlər/ are the larval stage of members of the order Lepidoptera (the insect order comprising butterflies and moths).

As with most common names, the application of the word is arbitrary, since the larvae of sawflies commonly are called caterpillars as well.[1][2] Both lepidopteran and symphytan larvae have eruciform body shapes.

Caterpillars of most species are herbivorous (folivorous), but not all; some (about 1%) are insectivorous, even cannibalistic. Some feed on other animal products; for example, clothes moths feed on wool, and horn moths feed on the hooves and horns of dead ungulates.

A monarch butterfly (*Danaus plexippus*) caterpillar feeding on an unopened seed pod of swamp milkweed

Caterpillars are typically voracious feeders and many of them are among the most serious of agricultural pests. In fact many moth species are best known in their caterpillar stages because of the damage they cause to fruits and other agricultural produce, whereas the moths are obscure and do no direct harm. Conversely, various species of caterpillar are valued as sources of silk, as human or animal food, or for biological control of pest plants.

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Etymology

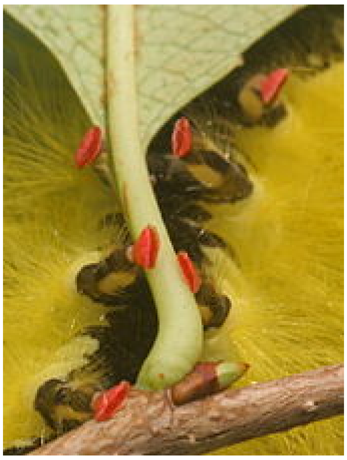
The origins of the word "caterpillar" date from the early 16th century. They derive from Middle English *catirpel*, *catirpeller*, probably an alteration of Old North French *catepelose*: *cate*, cat (from Latin *cattus*) + *pelose*, hairy (from Latin *pilōsus*).[3]

The inchworm, or looper caterpillars from the family Geometridae are so named because of the way they move, appearing to measure the earth (the word *geometrid* means *earth-measurer* in Greek);[4] the primary reason for this unusual locomotion is the elimination of nearly all the prolegs except the clasper on the terminal segment.

A geometrid caterpillar or inchworm

Description

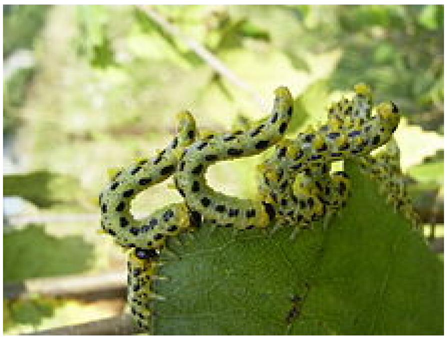
Caterpillars have soft bodies that can grow rapidly between moults. Their size varies between species and instars (moults) from as small as 1 mm up to 14 cm.[5] Some larvae of the order Hymenoptera (ants, bees and wasps) can appear like the caterpillars of the Lepidoptera. Such larvae are mainly seen in the sawfly suborder. However while these larvae superficially resemble caterpillars, they can be distinguished by the presence of prolegs on every abdominal segment, an absence of crochets or hooks on the prolegs (these are present on lepidopteran caterpillars), one pair of prominent ocelli on the head capsule, and an absence of the upside-down Y-shaped suture on the front of the head.[6]



Crochets on a caterpillar's prolegs

Lepidopteran caterpillars can be differentiated from sawfly larvae by:

- the numbers of pairs of pro-legs; sawfly larvae have 6 or more pairs while caterpillars have a maximum of 5 pairs.
- the number of stemmata (simple eyes); the sawfly larvae have only two,[7] while caterpillars usually have six.
- the presence of crochets on the prolegs; these are absent in the sawflies.
- sawfly larvae have an invariably smooth head capsule with no cleavage lines, while lepidopterous caterpillars bear an inverted "Y" or "V" (adfrontal suture).



Larvae of *Craesus septentrionalis*, a sawfly showing 6 pairs of pro-legs.

Fossils

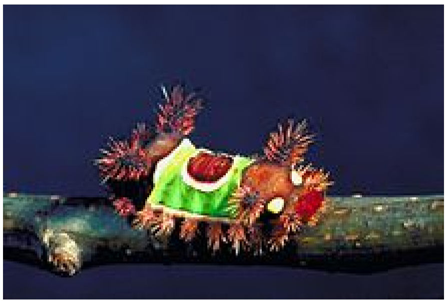
In 2019, a geometrid moth caterpillar dating back to the Eocene epoch, approximately 44 million years ago, was found preserved in Baltic amber. It was described under *Eogeometer vadens*.[8][9][10] Previously, another fossil dating back approximately 125 million years was found in Lebanese amber.[11][12]

Eogeometer vadens, the earliest known geometrid moth caterpillar found in Baltic amber[8][9][10]

Defenses

Many animals feed on caterpillars as they are rich in protein. As a result, caterpillars have evolved various means of defense.

Caterpillars have evolved defenses against physical conditions such as cold, hot or dry environmental conditions. Some Arctic species like *Gynaephora groenlandica* have special basking and aggregation behaviours[13] apart from physiological adaptations to remain in a dormant state.[14]



The saddleback caterpillar has urticating hair and aposematic colouring.

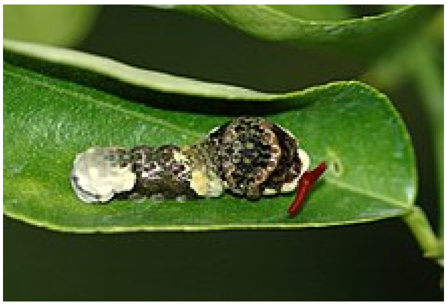
Appearance

Costa Rican hairy caterpillar. The spiny bristles are a self-defense mechanism

The appearance of a caterpillar can often repel a predator: its markings and certain body parts can make it seem poisonous, or bigger in size and thus threatening, or non-edible. Some types of caterpillars are indeed poisonous or distasteful and their bright coloring is aposematic. Others may mimic dangerous caterpillars or other animals while not being dangerous themselves. Many caterpillars are cryptically colored and resemble the plants on which they feed. An example of caterpillars that use camouflage for defence is the species *Nemoria arizonaria*. If the caterpillars hatch in the spring and feed on oak catkins they appear green. If they hatch in the summer they appear dark colored, like oak twigs. The differential development is linked to the tannin content in the diet.[15] Caterpillars may even have spines or growths that resemble plant parts such as thorns. Some look like objects in the environment such as bird droppings. Some Geometridae cover themselves in plant parts, while bagworms construct and live in a bag covered in sand, pebbles or plant material.

Chemical defenses

More aggressive self-defense measures are taken by some caterpillars. These measures include having spiny bristles or long fine hair-like setae with detachable tips that will irritate by lodging in the skin or mucous membranes.[6] However some birds (such as cuckoos) will swallow even the hairiest of caterpillars. Other caterpillars acquire toxins from their host plants that render them unpalatable to most of their predators. For instance, ornate moth caterpillars utilize pyrrolizidine alkaloids that they obtain from their food plants to deter predators.[16] The most aggressive caterpillar defenses are bristles associated with venom glands. These bristles are called urticating hairs. A venom which is among the most potent defensive chemicals in any animal is produced by the South American silk moth genus *Lonomia*. Its venom is an anticoagulant powerful enough to cause a human to hemorrhage to death (See Lonomiasis).[17] This chemical is being investigated for potential medical applications. Most urticating hairs range in effect from mild irritation to dermatitis. Example: Brown-tail moth.



Giant swallowtail caterpillar everting its osmeterium in defense

Plants contain toxins which protect them from herbivores, but some caterpillars have evolved countermeasures which enable them to eat the leaves of such toxic plants. In addition to being unaffected by the poison, the caterpillars sequester it in their body, making them highly toxic to predators. The chemicals are also carried on into the adult stages. These toxic species, such as the cinnabar moth (*Tyria jacobaeae*) and monarch (*Danaus plexippus*) caterpillars, usually advertise themselves with the danger colors of red, yellow and black, often in bright stripes (see aposematism). Any predator that attempts to eat a caterpillar with an aggressive defense mechanism will learn and avoid future attempts.

Some caterpillars regurgitate acidic digestive juices at attacking enemies. Many papilionid larvae produce bad smells from extrudable glands called osmeteria.

Defensive behaviors

Many caterpillars display feeding behaviors which allow the caterpillar to remain hidden from potential predators. Many feed in protected environments, such as enclosed inside silk galleries, rolled leaves or by mining between the leaf surfaces.

Caterpillars linked together into a "train"

Some caterpillars, like early instars of the tomato hornworm and tobacco hornworm, have long "whip-like" organs attached to the ends of their body. The caterpillar wiggles these organs to frighten away flies and predatory wasps.[18] Some caterpillars can evade predators by using a silk line and dropping off from branches when disturbed. Many species thrash about violently when disturbed to scare away potential predators. One species (*Amorpha juglandis*) even makes high pitched whistles that can scare away birds.[19]

Social behaviors and relationships with other insects

Some caterpillars obtain protection by associating themselves with ants. The Lycaenid butterflies are particularly well known for this. They communicate with their ant protectors by vibrations as well as chemical means and typically provide food rewards.[20]

Some caterpillars are gregarious; large aggregations are believed to help in reducing the levels of parasitization and predation.[21] Clusters amplify the signal of aposematic coloration, and individuals may participate in group regurgitation or displays. Pine processionary (*Thaumetopoea pityocampa*) caterpillars often link into a long train to move through trees and over the ground. The head of the lead caterpillar is visible, but the other heads can appear hidden.[22] Forest tent caterpillars cluster during periods of cold weather.

Predators

Caterpillars suffer predation from many animals. The European pied flycatcher is one species that preys upon caterpillars. The flycatcher typically finds caterpillars among oak foliage. Paper wasps, including those in the genus *Polistes* and *Polybia* catch caterpillars to feed their young and themselves.

Behavior

A pasture day moth caterpillar feeding on capeweed

Caterpillars have been called "eating machines", and eat leaves voraciously. Most species shed their skin four or five times as their bodies grow, and they eventually enter a pupal stage before becoming adults.[23] Caterpillars grow very quickly; for instance, a tobacco hornworm will increase its weight ten-thousandfold in less than twenty days. An adaptation that enables them to eat so much is a mechanism in a specialized midgut that quickly transports ions to the lumen (midgut cavity), to keep the potassium level higher in the midgut cavity than in the hemolymph.[24]

Most caterpillars are solely herbivorous. Many are restricted to feeding on one species of plant, while others are polyphagous. Some, including the clothes moth, feed on detritus. Some are predatory, and may prey on other species of caterpillars (e.g. Hawaiian *Eupithecia*). Others feed on eggs of other insects, aphids, scale insects, or ant larvae. A few are parasitic on cicadas or leaf hoppers (Epipyropidae).[25] Some Hawaiian caterpillars (*Hyposmocoma molluscivora*) use silk traps to capture snails.[26]

A gypsy moth caterpillar

Many caterpillars are nocturnal. For example, the "cutworms" (of the family Noctuidae) hide at the base of plants during the day and only feed at night.[27] Others, such as gypsy moth (Lymantria dispar) larvae, change their activity patterns depending on density and larval stage, with more diurnal feeding in early instars and high densities.[28]

Economic effects

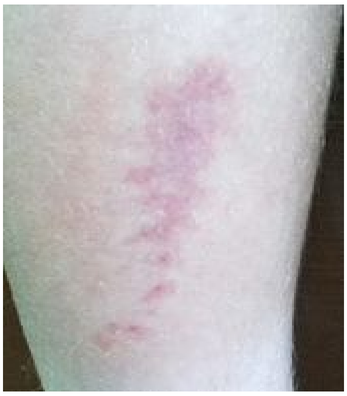
Hypsipyla grandela damages mahogany in Brazil

Caterpillars cause much damage, mainly by eating leaves. The propensity for damage is enhanced by monocultural farming practices, especially where the caterpillar is specifically adapted to the host plant under cultivation. The cotton bollworm causes enormous losses. Other species eat food crops. Caterpillars have been the target of pest control through the use of pesticides, biological control and agronomic practices. Many species have become resistant to pesticides. Bacterial toxins such as those from *Bacillus thuringiensis* which are evolved to affect the gut of Lepidoptera have been used in sprays of bacterial spores, toxin extracts and also by incorporating genes to produce them within the host plants. These approaches are defeated over time by the evolution of resistance mechanisms in the insects.[29]

Plants evolve mechanisms of resistance to being eaten by caterpillars, including the evolution of chemical toxins and physical barriers such as hairs. Incorporating host plant resistance (HPR) through plant breeding is another approach used in reducing the impact of caterpillars on crop plants.[30]

Some caterpillars are used in industry. The silk industry is based on the silkworm caterpillar.

Human health



Buck moth caterpillar sting on a shin twenty-four hours after occurrence in south Louisiana. The reddish mark covers an area about 20 mm at its widest point by about 70 mm in length.

Caterpillar hair can be a cause of human health problems. Caterpillar hairs sometimes have venoms in them and species from approximately 12 families of moths or butterflies worldwide can inflict serious human injuries ranging from urticarial dermatitis and atopic asthma to osteochondritis, consumption coagulopathy, renal failure, and intracerebral hemorrhage.[31] Skin rashes are the most common, but there have been fatalities.[32] *Lonomia* is a frequent cause of envenomation in Brazil, with 354 cases reported between 1989 and 2005. Lethality ranging up to 20% with death caused most often by intracranial hemorrhage.[33]

Caterpillar hair has also been known to cause kerato-conjunctivitis. The sharp barbs on the end of caterpillar hairs can get lodged in soft tissues and mucous membranes such as the eyes. Once they enter such tissues, they can be difficult to extract, often exacerbating the problem as they migrate across the membrane.[34]

This becomes a particular problem in an indoor setting. The hair easily enter buildings through ventilation systems and accumulate in indoor environments because of their small size, which makes it difficult for them to be vented out. This accumulation increases the risk of human contact in indoor environments.[35]

Caterpillars are a food source in some cultures. For example, in South Africa mopane worms are eaten by the bushmen, and in China silkworms are considered a delicacy.

In popular culture

In the Old Testament of the Bible caterpillars are feared as pest that devour crops. They are part of the "pestilence, blasting, mildew, locus" because of their association with the locust, thus they are one of the plagues of Egypt. Jeremiah names them as one of the inhabitants of Babylon. The English word caterpillar derives from the old French *catepelose* (hairy cat) but merged with the *piller* (pillager). Caterpillars became a symbol for social dependents. Shakespeare's Bolingbroke described King Richard's friends as "The caterpillars of the commonwealth, Which I have sworn to weed and pluck away". In 1790 William Blake referenced this popular image in The Marriage of Heaven and Hell when he attacked priests: "as the caterpillar chooses the fairest leaves to lay her eggs on, so the priest lay his curse on the fairest joys".[37]

William Blake's illustration of a caterpillar overlooking a child from his illustrated book *For Children The Gates of Paradise*.[36]

The role of caterpillars in the life stages of butterflies was badly understood. In 1679 Maria Sibylla Merian published the first volume of *The Caterpillars' Marvelous Transformation and Strange Floral Food*, which contained 50 illustrations and a description of insects, moths, butterflies and their larvae.[38] An earlier popular publication on moths and butterflies, and their caterpillars, by Jan Goedart had not included eggs in the life stages of European moths and butterflies, because he had believed that caterpillars were generated from water. When Merian published her study of caterpillars it was still widely believed that insects were spontaneously generated. Merian's illustrations supported the findings of Francesco Redi, Marcello Malpighi and Jan Swammerdam.[39]

A 1907 illustrations by Arthur Rackham of the Caterpillar talking to Alice in Alice's Adventures in Wonderland

Butterflies were regarded as symbol for the human soul since ancient time, and also in the Christian tradition.[40] Goedart thus located his empirical observations on the transformation of caterpillars into butterflies in the Christian tradition. As such he argued that the metamorphosis from caterpillar into butterfly was a symbol, and even proof, of Christ's resurrection. He argued "that from dead caterpillars emerge living animals; so it is equally true and miraculous, that our dead and rotten corpses will rise from the grave."[41] Swammerdam, who in 1669 had demonstrated that inside a caterpillar the rudiments of the future butterfly's limbs and wings could be discerned, attacked the mystical and religious notion that the caterpillar died and the butterfly subsequently resurrected.[42] As a militant Cartesian, Swammerdam attacked Goedart as ridiculous, and when publishing his findings he proclaimed "here we witness the digression of those who have tried to prove Resurrection of the Dead from these obviously natural and comprehensible changes within the creature itself."[43]

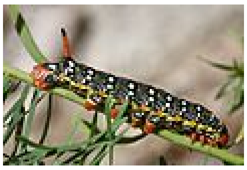
Since then the metamorphoses of the caterpillar into a butterfly has in Western societies been associated with countless human transformations in folktales and literature. There is no process in the physical life of human beings that resembles this metamorphoses, and the symbol of the caterpillar tends to depict a psychic transformation of a human. As such the caterpillar has in the Christian tradition become a metaphor for being "born again".[44]

Famously, in Lewis Carroll's Alice's Adventures in Wonderland a caterpillar asks Alice "Who are you?". When Alice comments on the caterpillar's inevitable transformation into a butterfly, the caterpillar champions the position that in spite of changes it is still possible to know something, and that Alice is the same Alice at the beginning and end of a considerable interval.[45] When the Caterpillar asks Alice to clarify a point, the child replies "I'm afraid I can't put it more clearly... for I can't but understand it myself, to begin with, and being so many different sizes in a day is very confusing". Here Carroll satirizes René Descartes, the founder of Cartesian philosophy, and his theory on innate ideas. Descartes argued that we are distracted by urgent bodily stimuli that swamp the human mind in childhood. Descartes also theorised that inherited preconceived opinions obstruct the human perception of the truth.[46]

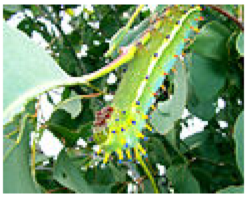
More recent symbolic references to caterpillars in popular media include the *Mad Men* season 3 episode "The Fog", in which Betty Draper has a drug-induced dream, while in labor, that she captures a caterpillar and holds it firmly in her hand.[47] In *The Sopranos* season 5 episode "The Test Dream", Tony Soprano dreams that Ralph Cifaretto has a caterpillar on his bald head that changes into a butterfly.

Gallery

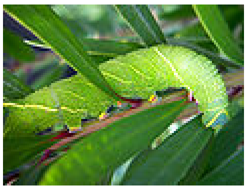
Click left or right for a slide show.



Caterpillar of the spurge hawk-moth, near Binn, Valais, Switzerland at c. 2 km altitude.



Caterpillar of the emperor gum moth.

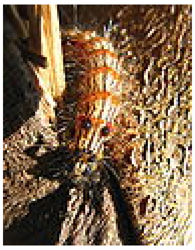


A poplar hawk-moth caterpillar (a common species of caterpillar in the UK).

Ant tending a lycaenid caterpillar.

Life cycle of the red-humped caterpillar (*Schizura concinna*).

Forest tent caterpillar (Malacosoma disstria)



Camouflage: apparently with eight eyes, only two of them are real. Photo in a eucalyptus tree, São Paulo, Brazil

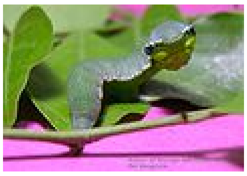
Caterpillar of the Polyphemus moth (*Antheraea polyphemus*), Virginia, United States

Caterpillars on an apple tree in Victoria, British Columbia, Canada

Caterpillar on a leaf

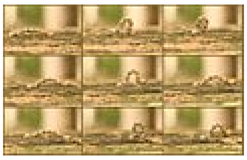
Caterpillar of Belize

Dryas iulia



Caterpillar of great orange tip resembling the common green vine snake (*Ahaetulla nasuta*)

Prepupa of cabbage looper in its cocoon



Locomotion of a small Geometrid caterpillar.

See also

- Edible caterpillars
- Larval food plants of Lepidoptera
- Lepidopterism - caterpillar dermatitis
- List of pests and diseases of roses
- Sericulture

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Grasshopper

Grasshoppers are a group of insects belonging to the suborder Caelifera. They are among what is probably the most ancient living group of chewing herbivorous insects, dating back to the early Triassic around 250 million years ago.

Grasshoppers are typically ground-dwelling insects with powerful hind legs which allow them to escape from threats by leaping vigorously. As hemimetabolous insects, they do not undergo complete metamorphosis; they hatch from an egg into a nymph or "hopper" which undergoes five moults, becoming more similar to the adult insect at each developmental stage. At high population densities and under certain environmental conditions, some grasshopper species can change color and behavior and form swarms. Under these circumstances, they are known as locusts.

Grasshoppers are plant-eaters, with a few species at times becoming serious pests of cereals, vegetables and pasture, especially when they swarm in their millions as locusts and destroy crops over wide areas. They protect themselves from predators by camouflage; when detected, many species attempt to startle the predator with a brilliantly-coloured wing-flash while jumping and (if adult) launching themselves into the air, usually flying for only a short distance. Other species such as the rainbow grasshopper have warning coloration which deters predators. Grasshoppers are affected by parasites and various diseases, and many predatory creatures feed on both nymphs and adults. The eggs are subject to attack by parasitoids and predators.

Grasshoppers have had a long relationship with humans. Swarms of locusts can have devastating effects and cause famine, and even in smaller numbers, the insects can be serious pests. They are used as food in countries such as Mexico and Indonesia. They feature in art, symbolism and literature.

Grasshopper

Temporal range: 252 Ma–Recent

American grasshopper (*Schistocerca americana*)

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Orthoptera
Suborder:	Caelifera
Infraorder:	Acrididea
Informal group:	Acridomorpha Dirsh, 1966

Superfamilies

- Acridoidea
- Eumastacoidea
- Pneumoroidea
- Proscopioidea
- Pyrgomorphoidea
- Tanaoceroidea
- Trigonopterygoidea

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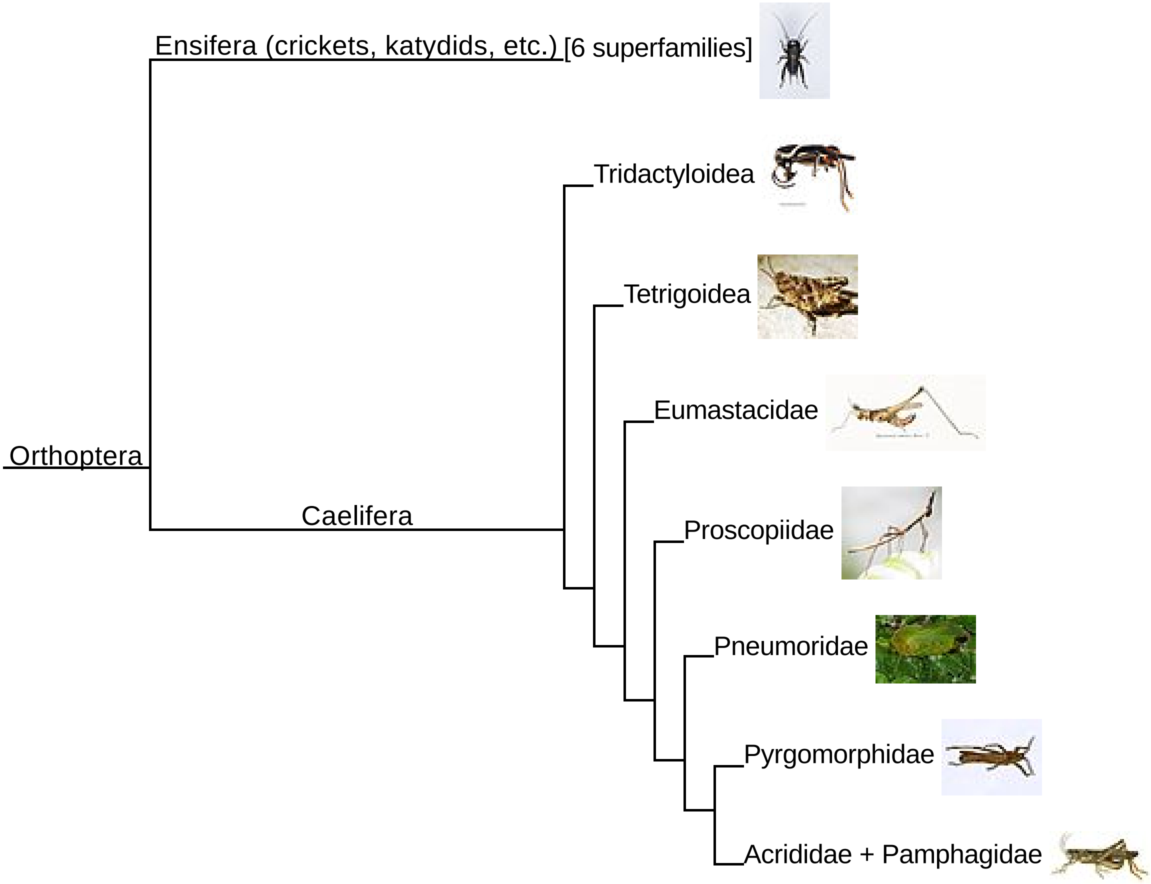
Phylogeny

Grasshoppers belong to the suborder Caelifera. Although, "grasshopper" is sometimes used as a common name for the suborder in general,[1][2][3] some sources restrict it to the more "advanced" groups.[4] They may be placed in the infraorder Acrididea[5] and have been referred-to as "short-horned grasshoppers" in older texts[6] to distinguish them from the also-obsolete term "long-horned grasshoppers" (now bush-crickets or katydids) with their much longer antennae. The phylogeny of the Caelifera, based on mitochondrial ribosomal RNA of thirty-two taxa in six out of seven superfamilies, is shown as a cladogram. The Ensifera (crickets, *etc.*), Caelifera and all the superfamilies of grasshoppers except Pamphagoidea appear to be monophyletic.[7][8]



Fossil grasshoppers at the Royal Ontario Museum

In evolutionary terms, the split between the Caelifera and the Ensifera is no more recent than the Permo-Triassic boundary;[9] the earliest insects that are certainly Caeliferans are in the extinct families Locustopseidae and Locustavidae from the early Triassic, roughly 250 million years ago. The group diversified during the Triassic and have remained important plant-eaters from that time to now. The first modern families such as the Eumastacidae, Tetrigidae and Tridactylidae appeared in the Cretaceous, though some insects that might belong to the last two of these groups are found in the early Jurassic.[10][11] Morphological classification is difficult because many taxa have converged towards a common habitat type; recent taxonomists have concentrated on the internal genitalia, especially those of the male. This information is not available from fossil specimens, and the palaentological taxonomy is founded principally on the venation of the hindwings.[12]

The Caelifera includes some 2,400 valid genera and about 11,000 known species. Many undescribed species probably exist, especially in tropical wet forests. The Caelifera have a predominantly tropical distribution with fewer species known from temperate zones, but most of the superfamilies have representatives worldwide. They are almost exclusively herbivorous and are probably the oldest living group of chewing herbivorous insects.[12]

The most diverse superfamily is the Acridoidea, with around 8,000 species. The two main families in this are the Acrididae (grasshoppers and locusts) with a worldwide distribution, and the Romaleidae (lubber grasshoppers), found chiefly in the New World. The Ommexechidae and Tristiridae are South American, and the Lentulidae, Lithidiidae and Pamphagidae are mainly African. The Pauliniids are nocturnal and can swim or skate on water, and the Lentulids are wingless.[10] Pneumoridae are native to Africa, particularly southern Africa, and are distinguished by the inflated abdomens of the males.[13]

Characteristics

Grasshoppers have the typical insect body plan of head, thorax and abdomen. The head is held vertically at an angle to the body, with the mouth at the bottom. The head bears a large pair of compound eyes which give all-round vision, three simple eyes which can detect light and dark, and a pair of thread-like antennae that are sensitive to touch and smell. The downward-directed mouthparts are modified for chewing and there are two sensory palps in front of the jaws.[14]

The thorax and abdomen are segmented and have a rigid cuticle made up of overlapping plates composed of chitin. The three fused thoracic segments bear three pairs of legs and two pairs of wings. The forewings, known as tegmina, are narrow and leathery while the hindwings are large and membranous, the veins providing strength. The legs are terminated by claws for gripping. The hind leg is particularly powerful; the femur is robust and has several ridges where different surfaces join and the inner ridges bear stridulatory pegs in some species. The posterior edge of the tibia bears a double row of spines and there are a pair of articulated spurs near its lower end. The interior of the thorax houses the muscles that control the wings and legs.[14]

The abdomen has eleven segments, the first of which is fused to the thorax and contains the tympanal organ and hearing system. Segments two to eight are ring-shaped and joined by flexible membranes. Segments nine to eleven are reduced in size; segment nine bears a pair of cerci and segments ten and eleven house the reproductive organs. Female grasshoppers are normally larger than males, with short ovipositors.[14] The name of the suborder "Caelifera" comes from the Latin and means *chisel-bearing*, referring to the shape of the ovipositor.[15]

Those species that make easily heard noises usually do so by rubbing a row of pegs on the hind legs against the edges of the forewings (stridulation). These sounds are produced mainly by males to attract females, though in some species the females also stridulate.[16]

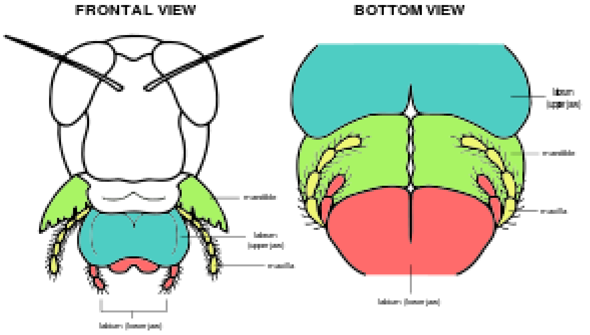
Grasshoppers may be confused with crickets, but they differ in many aspects; these include the number of segments in their antennae and the structure of the ovipositor, as well as the location of the tympanal organ and the methods by which sound is produced.[17] Ensiferans have antennae that can be much longer than the body and have at least 20–24 segments, while caeliferans have fewer segments in their shorter, stouter antennae.[16]

Ensifera, like this great green bush-cricket *Tettigonia viridissima*, somewhat resemble grasshoppers but have over 20 segments in their antennae and different ovipositors.

Biology

Diet and digestion

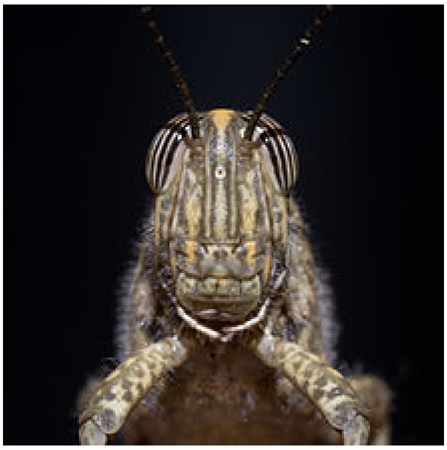
Most grasshoppers are polyphagous, eating vegetation from multiple plant sources,[18] but some are omnivorous and also eat animal tissue and animal faeces. In general their preference is for grasses, including many cereals grown as crops.[19] The digestive system is typical of insects, with Malpighian tubules discharging into the midgut. Carbohydrates are digested mainly in the crop, while proteins are digested in the ceca of the midgut. Saliva is abundant but largely free of enzymes, helping to move food and Malpighian secretions along the gut. Some grasshoppers possess cellulase, which by softening plant cell walls makes plant cell contents accessible to other digestive enzymes.[20]



Structure of mouthparts

Sensory organs

Grasshoppers have a typical insect nervous system, and have an extensive set of external sense organs. On the side of the head are a pair of large compound eyes which give a broad field of vision and can detect movement, shape, colour and distance. There are also three simple eyes (ocelli) on the forehead which can detect light intensity, a pair of antennae containing olfactory (smell) and touch receptors, and mouthparts containing gustatory (taste) receptors.[21] At the front end of the abdomen there is a pair of tympanal organs for sound reception. There are numerous fine hairs (setae) covering the whole body that act as mechanoreceptors (touch and wind sensors), and these are most dense on the antennae, the palps (part of the mouth), and on the cerci at the tip of the abdomen.[22] There are special receptors (campaniform sensillae) embedded in the cuticle of the legs that sense pressure and cuticle distortion.[23] There are internal "chordotonal" sense organs specialized to detect position and movement about the joints of the exoskeleton. The receptors convey information to the central nervous system through sensory neurons, and most of these have their cell bodies located in the periphery near the receptor site itself.[22]



Frontal view of Egyptian locust (*Anacridium aegyptium*) showing the compound eyes, tiny ocelli and numerous setae

Circulation and respiration

Like other insects, grasshoppers have an open circulatory system and their body cavities are filled with haemolymph. A heart-like structure in the upper part of the abdomen pumps the fluid to the head from where it percolates past the tissues and organs on its way back to the abdomen. This system circulates nutrients throughout the body and carries metabolic wastes to be excreted into the gut. Other functions of the haemolymph include wound healing, heat transfer and the provision of hydrostatic pressure, but the circulatory system is not involved in gaseous exchange.[24] Respiration is performed using tracheae, air-filled tubes, which open at the surfaces of the thorax and abdomen through pairs of valved spiracles. Larger insects may need to actively ventilate their bodies by opening some spiracles while others remain closed, using abdominal muscles to expand and contract the body and pump air through the system.[25]

Jumping

A large grasshopper, such as a locust, can jump about a metre (twenty body lengths) without using its wings; the acceleration peaks at about 20 g.[26] Grasshoppers jump by extending their large back legs and pushing against the substrate (the ground, a twig, a blade of grass or whatever else they are standing on); the reaction force propels them into the air.[27] They jump for several reasons; to escape from a predator, to launch themselves into flight, or simply to move from place to place. For the escape jump in particular there is strong selective pressure to maximize take-off velocity, since this determines the range. This means that the legs must thrust against the ground with both high force and a high velocity of movement. A fundamental property of muscle is that it cannot contract with high force and high velocity at the same time. Grasshoppers overcome this by using a catapult mechanism to amplify the mechanical power produced by their muscles.[28]

The jump is a three-stage process.[29] First, the grasshopper fully flexes the lower part of the leg (tibia) against the upper part (femur) by activating the flexor tibiae muscle (the back legs of the grasshopper in the top photograph are in this preparatory position). Second, there is a period of co-contraction in which force builds up in the large, pennate extensor tibiae muscle, but the tibia is kept flexed by the simultaneous contraction of the flexor tibiae muscle. The extensor muscle is much stronger than the flexor muscle, but the latter is aided by specialisations in the joint that give it a large effective mechanical advantage over the former when the tibia is fully flexed.[30] Co-contraction can last for up to half a second, and during this period the extensor muscle shortens and stores elastic strain energy by distorting stiff cuticular structures in the leg.[31] The extensor muscle contraction is quite slow (almost isometric), which allows it to develop high force (up to 14 N in the desert locust), but because it is slow only low power is needed. The third stage of the jump is the trigger relaxation of the flexor muscle, which releases the tibia from the flexed position. The subsequent rapid tibial extension is driven mainly by the relaxation of the elastic structures, rather than by further shortening of the extensor muscle. In this way the stiff cuticle acts like the elastic of a catapult, or the bow of a bow-and-arrow. Energy is put into the store at low power by slow but strong muscle contraction, and retrieved from the store at high power by rapid relaxation of the mechanical elastic structures.[32][33]

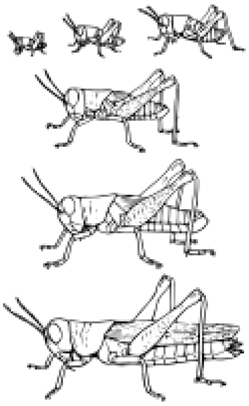
Stridulation

Male grasshoppers spend much of the day stridulating, singing more actively under optimal conditions and being more subdued when conditions are adverse; females also stridulate, but their efforts are insignificant when compared to the males. Late-stage male nymphs can sometimes be seen making stridulatory movements, although they lack the equipment to make sounds, demonstrating the importance of this behavioural trait. The songs are a means of communication; the male stridulation seems to express reproductive maturity, the desire for social cohesion and individual well-being. Social cohesion becomes necessary among grasshoppers because of their ability to jump or fly large distances, and the song can serve to limit dispersal and guide others to favourable habitat. The generalised song can vary in phraseology and intensity, and is modified in the presence of a rival male, and changes again to a courtship song when a female is nearby.[34] In male grasshoppers of the family Pneumoridae, the enlarged abdomen amplifies stridulation.[13]

Life cycle

In most grasshopper species, conflicts between males over females rarely escalate beyond ritualistic displays. Some exceptions include the chameleon grasshopper (*Kosciuscola tristis*), where males may fight on top of ovipositing females; engaging in leg grappling, biting, kicking and mounting.[35]

Romalea microptera grasshoppers: female (larger) is laying eggs, with male in attendance.



Six stages (instars) of development, from newly hatched nymph to fully winged adult

The newly emerged female grasshopper has a preoviposition period of a week or two while she increases in weight and her eggs mature. After mating, the female of most species digs a hole with her ovipositor and lays a batch of eggs in a pod in the ground near food plants, generally in the summer. After laying the eggs, she covers the hole with soil and litter.[14] Some, like the semi-aquatic *Cornops aquaticum*, deposit the pod directly into plant tissue.[36] The eggs in the pod are glued together with a froth in some species. After a few weeks of development, the eggs of most species in temperate climates go into diapause, and pass the winter in this state. Diapause is broken by a sufficiently low ground temperature, with development resuming as soon as the ground warms above a certain threshold temperature. The embryos in a pod generally all hatch out within a few minutes of each other. They soon shed their membranes and their exoskeletons harden. These first instar nymphs can then jump away from predators.[37]

Grasshoppers undergo incomplete metamorphosis: they repeatedly moult, each instar becoming larger and more like an adult, with the wing-buds increasing in size at each stage. The number of instars varies between species but is often six. After the final moult, the wings are inflated and become fully functional. The migratory grasshopper, *Melanoplus sanguinipes*, spends about 25 to 30 days as a nymph, depending on sex and temperature, and lives for about 51 days as an adult.[37]

Swarming

Millions of plague locusts on the move in Australia

Locusts are the swarming phase of certain species of short-horned grasshoppers in the family Acrididae. Swarming behaviour is a response to overcrowding. Increased tactile stimulation of the hind legs causes an increase in levels of serotonin.[38] This causes the grasshopper to change colour, feed more and breed faster. The transformation of a solitary individual into a swarming one is induced by several contacts per minute over a short period.[39]

Following this transformation, under suitable conditions dense nomadic bands of flightless nymphs known as "hoppers" can occur, producing pheromones which attract the insects to each other. With several generations in a year, the locust population can build up from localised groups into vast accumulations of flying insects known as plagues, devouring all the vegetation they encounter. The largest recorded locust swarm was one formed by the now-extinct Rocky Mountain locust in 1875; the swarm was 1,800 miles (2,900 km) long and 110 miles (180 km) wide,[40] and one estimate puts the number of locusts involved at 3.5 trillion.[41] An adult desert locust can eat about 2 g (0.1 oz) of plant material each day, so the billions of insects in a large swarm can be very destructive, stripping all the foliage from plants in an affected area and consuming stems, flowers, fruits, seeds and bark.[42]

Predators, parasites and pathogens

Grasshoppers have a wide range of predators at different stages of their lives; eggs are eaten by bee-flies, ground beetles and blister beetles; hoppers and adults are taken by other insects such as ants, robber flies and sphecid wasps, by spiders, and by many birds and small mammals including dogs and cats.[43]

Cottontop tamarin monkey eating a grasshopper

The eggs and nymphs are under attack by parasitoids including blow flies, flesh flies, and tachinid flies. External parasites of adults and nymphs include mites.[43] Female grasshoppers parasitised by mites produce fewer eggs and thus have fewer offspring than unaffected individuals.[44]

Grasshopper with parasitic mites

The grasshopper nematode (*Mermis nigrescens*) is a long slender worm that infects grasshoppers, living in the insect's hemocoel. Adult worms lay eggs on plants and the host becomes infected when the foliage is eaten.[45] *Spinochordodes tellinii* and *Paragordius tricuspidatus* are parasitic worms that infect grasshoppers and alter the behaviour of their hosts. When the worms are sufficiently developed, the grasshopper is persuaded to leap into a nearby body of water where it drowns, thus enabling the parasite to continue with the next stage of its life cycle, which takes place in water.[46][47]

Grasshoppers are affected by diseases caused by bacteria, viruses, fungi and protozoa. The bacteria *Serratia marcescens* and *Pseudomonas aeruginosa* have both been implicated in causing disease in grasshoppers, as has the entomopathogenic fungus *Beauveria bassiana*. This widespread fungus has been used to control various pest insects around the world, but although it infects grasshoppers, the infection is not usually lethal because basking in the sun has the result of raising the insect's temperature above a threshold tolerated by the fungus.[49] The fungal pathogen *Entomophaga grylli* is able to influence the behaviour of its grasshopper host, causing it to climb to the top of a plant and cling to the stem as it dies. This ensures wide dispersal of the fungal spores liberated from the corpse.[50]

Locusts killed by the naturally occurring fungus *Metarhizium*, an environmentally friendly means of biological control. CSIRO, 2005[48]

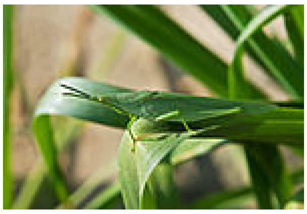
The fungal pathogen *Metarhizium acridum* is found in Africa, Australia and Brazil where it has caused epizootics in grasshoppers. It is being investigated for possible use as a microbial insecticide for locust control.[49] The microsporidian fungus *Nosema locustae*, once considered to be a protozoan, can be lethal to grasshoppers. It has to be consumed by mouth and is the basis for a bait-based commercial microbial pesticide. Various other microsporidians and protozoans are found in the gut.[49]

Anti-predator defences

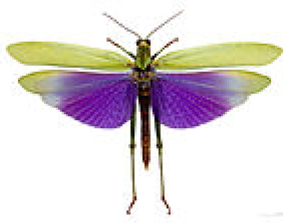
Grasshoppers exemplify a range of anti-predator adaptations, enabling them to avoid detection, to escape if detected, and in some cases to avoid being eaten if captured. Grasshoppers are often camouflaged to avoid detection by predators that hunt by sight; some species can change their coloration to suit their surroundings.[51]

Several species such as the hooded leaf grasshopper *Phyllochoreia ramakrishnai* (Eumastacoidea) are detailed mimics of leaves. Stick grasshoppers (Proscopiidae) mimic wooden sticks in form and coloration.[52] Grasshoppers often have deimatic patterns on their wings, giving a sudden flash of bright colours that may startle predators long enough to give time to escape in a combination of jump and flight.[53]

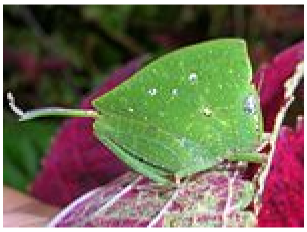
Some species are genuinely aposematic, having both bright warning coloration and sufficient toxicity to dissuade predators. *Dictyophorus productus* (Pyrgomorphidae) is a "heavy, bloated, sluggish insect" that makes no attempt to hide; it has a bright red abdomen. A *Cercopithecus* monkey that ate other grasshoppers refused to eat the species.[54] Another species, the rainbow or painted grasshopper of Arizona, *Dactylotum bicolor* (Acridoidea), has been shown by experiment with a natural predator, the little striped whiptail lizard, to be aposematic.[55]



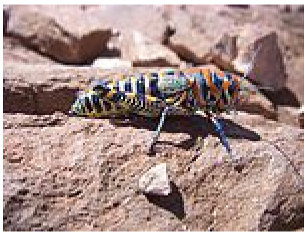
Gaudy grasshopper, *Atractomorpha lata*, evades predators with camouflage.



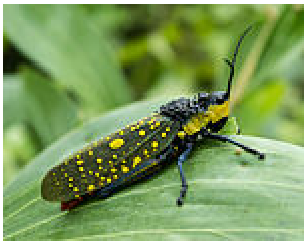
Lubber grasshopper, *Titanacris albipes*, has deimatically coloured wings, used to startle predators.



Leaf grasshopper, *Phyllochoreia ramakrishnai*, mimics a green leaf.



Painted grasshopper, *Dactylotum bicolor*, deters predators with warning coloration.



Spotted grasshopper, *Aularches miliaris*, defends itself with toxic foam and warning colours.[56]

Relationship with humans

In art and media

Detail of grasshopper on table in Rachel Ruysch's painting *Flowers in a Vase*, c. 1685. National Gallery, London

Grasshoppers are occasionally depicted in artworks, such as the Dutch Golden Age painter Balthasar van der Ast's still life oil painting, *Flowers in a Vase with Shells and Insects*, c. 1630, now in the National Gallery, London, though the insect may be a bush-cricket.[57]

Another orthopteran is found in Rachel Ruysch's still life *Flowers in a Vase*, c. 1685. The seemingly static scene is animated by a "grasshopper on the table that looks about ready to spring", according to the gallery curator Betsy Wieseman, with other invertebrates including a spider, an ant, and two caterpillars.[58][59]

Grasshoppers are also featured in cinema. The 1957 film *Beginning of the End* portrayed giant grasshoppers attacking Chicago.[60] In the 1998 Disney/Pixar animated film *A Bug's Life*, the heroes are Flik and the ant colony, and Hopper and his henchmen are the grasshoppers.[61]

Symbolism

Sir Thomas Gresham's gilded grasshopper symbol, Lombard Street, London, 1563

Grasshoppers are sometimes used as symbols.[62] During the Greek Archaic Era, the grasshopper was the symbol of the *polis* of Athens,[63] possibly because they were among the most common insects on the dry plains of Attica.[63] Native Athenians for a while wore golden grasshopper brooches to symbolise that they were of pure Athenian lineage with no foreign ancestors.[63] Another symbolic use of the grasshopper is Sir Thomas Gresham's gilded grasshopper in Lombard Street, London, dating from 1563;[a] the building was for a while the headquarters of the Guardian Royal Exchange, but the company declined to use the symbol for fear of confusion with the locust.[64]

When grasshoppers appear in dreams, these have been interpreted as symbols of "Freedom, independence, spiritual enlightenment, inability to settle down or commit to decision". Locusts are taken literally to mean devastation of crops in the case of farmers; figuratively as "wicked men and women" for non-farmers; and "Extravagance, misfortune, & ephemeral happiness" by "gypsies".[65]

As food

In some countries, grasshoppers are used as food.[66] In southern Mexico, grasshoppers, known as *chapulines*, are eaten in a variety of dishes, such as in tortillas with chilli sauce.[67] Grasshoppers are served on skewers in some Chinese food markets, like the Donghuamen Night Market.[68] Fried grasshoppers (*walang goreng*) are eaten in the Gunung Kidul Regency, Yogyakarta, Java in Indonesia.[69] In America, the Ohlone burned grassland to herd grasshoppers into pits where they could be collected as food.[70]

Fried grasshoppers from Gunung Kidul, Yogyakarta, Indonesia

It is recorded in the Bible that John the Baptist ate locusts and wild honey (Greek: ἀκρίδες καὶ μέλι ἄγριον, *akrídes kaì méli ágrion*) while living in the wilderness.[71] However, because of a tradition of depicting him as an ascetic, attempts have been made to explain that the *locusts* were in fact a suitably ascetic vegetarian food such as carob beans, notwithstanding the fact that the word *ἀκρίδες* means plainly *grasshoppers*.[72][73]

As pests

Crop pest: grasshopper eating a maize leaf

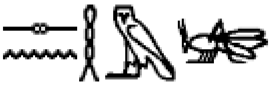
Grasshoppers eat large quantities of foliage both as adults and during their development, and can be serious pests of arid land and prairies. Pasture, grain, forage, vegetable and other crops can be affected. Grasshoppers often bask in the sun, and thrive in warm sunny conditions, so drought stimulates an increase in grasshopper populations. A single season of drought is not normally sufficient to stimulate a major population increase, but several successive dry seasons can do so, especially if the intervening winters are mild so that large numbers of nymphs survive. Although sunny weather stimulates growth, there needs to be an adequate food supply for the increasing grasshopper population. This means that although precipitation is needed to stimulate plant growth, prolonged periods of cloudy weather will slow nymphal development.[74]

Grasshoppers can best be prevented from becoming pests by manipulating their environment. Shade provided by trees will discourage them and they may be prevented from moving onto developing crops by removing coarse vegetation from fallow land and field margins and discouraging thick growth beside ditches and on roadside verges. With increasing numbers of grasshoppers, predator numbers may increase, but this seldom happens rapidly enough to have much effect on populations. Biological control is being investigated, and spores of the protozoan parasite *Nosema locustae* can be used mixed with bait to control grasshoppers, being more effective with immature insects.[75] On a small scale, neem products can be effective as a feeding deterrent and as a disruptor of nymphal development. Insecticides can be used, but adult grasshoppers are difficult to kill, and as they move into fields from surrounding rank growth, crops may soon become reinfested.[74]

Some grasshopper species, like the Chinese rice grasshopper, are a pest in rice paddies. Ploughing exposes the eggs on the surface of the field, to be destroyed by sunshine or eaten by natural enemies. Some eggs may be buried too deeply in the soil for hatching to take place.[76]

Locust plagues can have devastating effects on human populations, causing famines and population upheavals. They are mentioned in both the Koran and the Bible and have also been held responsible for cholera epidemics, resulting from the corpses of locusts drowned in the Mediterranean Sea and decomposing on beaches.[42] The FAO and other organisations monitor locust activity around the world. Timely application of pesticides can prevent nomadic bands of hoppers from forming before dense swarms of adults can build up.[77] Besides conventional control using contact insecticides,[77] biological pest control using the entomopathogenic fungus *Metarhizium acridum*, which specifically infects grasshoppers, has been used with some success.[78]

In literature


Egyptian hieroglyphs "snḥm"

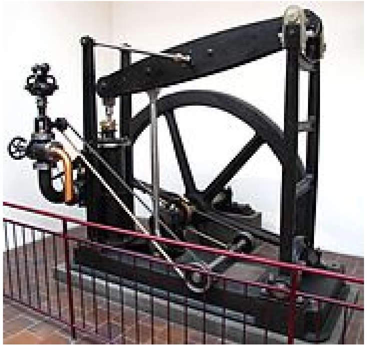
The Egyptian word for locust or grasshopper was written *snḥm* in the consonantal hieroglyphic writing system. The pharaoh Ramesses II compared the armies of the Hittites to locusts: "They covered the mountains and valleys and were like locusts in their multitude."[79]

One of Aesop's Fables, later retold by La Fontaine, is the tale of *The Ant and the Grasshopper*. The ant works hard all summer, while the grasshopper plays. In winter, the ant is ready but the grasshopper starves. Somerset Maugham's short story "The Ant and the Grasshopper" explores the fable's symbolism via complex framing.[80] Other human weaknesses besides improvidence have become identified with the grasshopper's behaviour.[65] So an unfaithful woman (hopping from man to man) is "a grasshopper" in "Poprygunya", an 1892 short story by Anton Chekhov,[81] and in Jerry Paris's 1969 film *The Grasshopper*.[82][83]

In mechanical engineering

The name "Grasshopper" was given to the Aeronca L-3 and Piper L-4 light aircraft, both used for reconnaissance and other support duties in World War II. The name is said to have originated when Major General Innis P. Swift saw a Piper making a rough landing and remarked that it looked like a "damned grasshopper" for its bouncing progress.[83][84][85]

Grasshopper beam engines were beam engines pivoted at one end, the long horizontal arm resembling the hind leg of a grasshopper. The type was patented by William Freemantle in 1803.[86][87][88]


A grasshopper beam engine, 1847

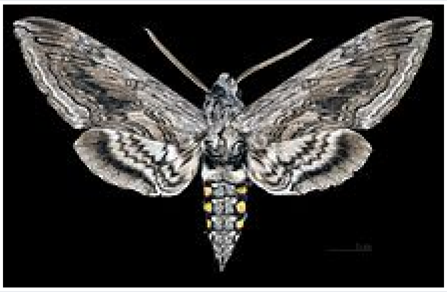
Notes

a. The symbol is a wordplay on the name Gresham and "grass".[62]

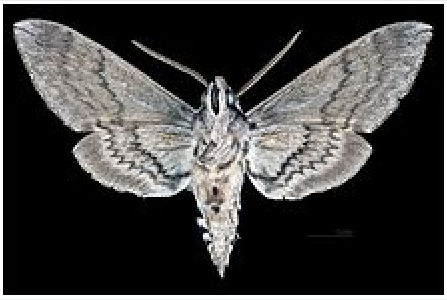
Manduca quinquemaculata

Manduca quinquemaculata, the **five-spotted hawkmoth**, is a brown and gray hawk moth of the family Sphingidae. The caterpillar, often referred to as the **tomato hornworm**, can be a major pest in gardens; they get their name from a dark projection on their posterior end and their use of tomatoes as host plants. Tomato hornworms are closely related to (and sometimes confused with) the tobacco hornworm *Manduca sexta*. This confusion arises because caterpillars of both species have similar morphologies and feed on the foliage of various plants from the family Solanaceae, so either species can be found on tobacco or tomato leaves. Because of this, the plant on which the caterpillar is found does not indicate its species.

Manduca quinquemaculata



Male - dorsal view



Male - ventral view

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Lepidoptera
Family:	Sphingidae
Genus:	*Manduca*
Species:	***M. quinquemaculata***

Binomial name

Manduca quinquemaculata
(Haworth, 1803)[1]

Synonyms

- *Sphinx 5-maculatus* Haworth, 1803
- *Phlegethontius quinquemaculatus*
- *Protoparce quinquemaculatus*

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Range

M. quinquemaculata is found across North America and Australia. The tobacco hornworm, a close relative of the tomato hornworm, tends to dominate the south while tomato hornworms are more prevalent in the northern United States.[2]

Food plants

- *Phlegethontius celeus* Hübner, 1821
- *Protoparce quinquemaculatus wirti* Schaus, 1927

Larva

Tomato hornworms are known to eat various plants from the family Solanaceae, commonly feeding on tomato, eggplant, pepper, tobacco, moonflowers and potato. Females prefer to oviposit on young leaves near the stem of host plants, and early instar caterpillars can often be found here during the day.[3] In the evening or early morning when sunlight is less direct, the caterpillars will feed on more distal leaves.[4]

Adult

Adult diet

Adults feed on nectar from flowering plants including *Datura meteloides,*[5] *Oenothera caespitosa,* and *Mirabilis multiflora.* Most of the food plants they target have large, fragrant white flowers.[6]

Interactions with host plants

Hawkmoths, including *M. quinquemaculata,* are the primary pollinators of *D. meteloides.* The length of the moth’s proboscis (around 10 cm), which is an elongated, tubular mouthpart used for sucking and feeding, is well-suited for retrieving nectar from the flowers. Aside from being a host plant for *M. quinquemaculata, D. meteloides* has also been used by humans for its opioid effects. *D. meteloides* contains tropane alkaloids, which are present throughout the plant including in the flowers.[5] These alkaloids have an intoxicating effects on the moth, which displays erratic flight patterns as well as uncoordinated, and often unsuccessful, landing attempts after consuming the nectar. Despite the impairment the nectar causes, the moths have been observed returning to the flowers and consuming more nectar. It has been hypothesized that the “spiked” nectar offers the moths reward beyond just nutrients.[5]

Both *Mirabilis multiflora* and *Oenothera caespitosa* are also dependent on hawkmoths for pollination. *M. quinquemaculata* has been found to feed from *Oenothera caespitosa* first and only later to visit *Mirabilis multiflora,* indicating a preference for the former.[6]

Life cycle

Oviposition

Females lay eggs singly on the surface of host plant leaves in late spring. Larvae hatch after approximately one week.[7] The female decides where to lay eggs based on an assessment of the risk of predation her offspring will face. On the tobacco plant *Nicotiana attenuata,* young leaves close to a plant's stem are more protected from predators and larvae that grow there gain more mass than larvae grown elsewhere on the plant; females prefer to oviposit, or lay their eggs, on these leaves.[3] Eggs are large and range in color from pale green to off-white.[4]

Larva

M. quinquemaculata larvae are large green caterpillars reaching a length of up to 10 cm when fully grown.[7] The caterpillars have a dark, pointed projection on their rear end that earns them the name "hornworm".[7] Although the tomato hornworm, *M. quinquemaculata,* can be confused with the tobacco hornworm, *M. sexta,* the larvae of these species can be distinguished by their lateral markings: tomato hornworms have eight V-shaped white markings with no borders and dark blue or black horns, while tobacco hornworms have seven white diagonal lines with a black border and red horns.[8]

Caterpillars hatch in late spring to early summer. They develop through five instars to reach maturity.[3][7] In warmer climates where the first generation emerges earlier in the year, two generations of caterpillars can coexist in a single summer.[4] Once fully grown, caterpillars fall from their host plants to pupate.[7]

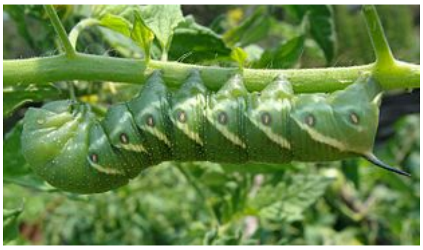
Pupa

Caterpillars pupate in early fall, which means they enter a stage of their life cycle where they become a pupa and undergo transformation into a moth.[7] After pupation, *M. quinquemaculata* overwinter in the soil near their host plants, with adults emerging the following summer.[9][4]

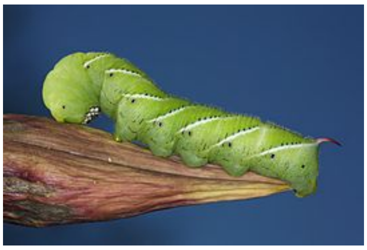
Adults

Adults are large, with a wingspan of up to 13 cm.[7] The wings of the moth are brown and gray with large mottled front wings and smaller hindwings with light and dark zig-zag patterned bands. The abdomens are brown and white with a row of five yellow spots down each side, giving them the name "five-spotted hawkmoth."[10][4] The moths of *M. quinquemaculata* and *M. sexta* can be distinguished by the number of spots on their abdomens.[8]

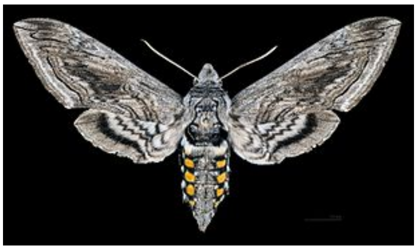
Shortly after adults emerge from the soil, they mate and females lay their eggs on host plants, renewing the life cycle.[7]



Tomato hornworm larva



closely related tobacco hornworm - note the red horn and lack of V-shaped white markings



Female - dorsal view

Female - ventral view

Relationship with *M. sexta*

M. quinquemaculata and *M. sexta* are both large hawkmoths of the genus *Manduca.* The two species have similar appearances in both larvae and adults and share common food sources, including tobacco.[4][11] Past research, observing that the two species are similar, referred to the two as sister species. However, a recent phylogenetic analysis from Kawahara et al. (2013) found that the two species, though closely related, are not sister species. The authors tracked the ancestral origin of both species to Central America, where the two species diverged from one another.[12]

Pest control

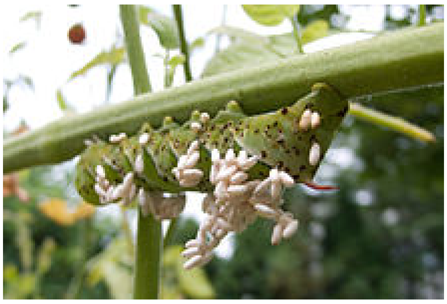
Because the larvae are pests of crop plants such as tomatoes and tobacco, biological control agents and traps have been used to control their populations. Gardeners whose tomato plants are predated by the tomato hornworm pick the caterpillars off of their plants.[4] Some gardeners plant marigolds, which repel the species, near their tomato plants to reduce predation.[13]

Parasites

The parasitoid wasp *Trichogramma* attacks *M. quinquemaculata* eggs. The larvae of the wasp develop in the egg, preventing the development of the caterpillar larvae. *Trichogramma* is a natural enemy of the *M. quinquemaculata* and has also been used as a biological control agent by humans.[14]

Braconidae wasp

A second parasitoid wasp, *Cotesia congregata* of the family Braconidae, also kills *M. quinquemaculata*. Adult females lay their eggs inside the skin of the hornworm caterpillar. After hatching, the wasp larvae use the organs and tissues of the caterpillar as food sources before burrowing out of the skin and pupating on the back and sides of the caterpillar. Once the wasps have emerged from their cocoons, the weakened caterpillar dies. Like the parasitoid wasp mentioned above, these wasps have also been suggested as a means of biological control of the tomato hornworm.[15][16]



closely related tobacco hornworm parasitized by braconid wasp

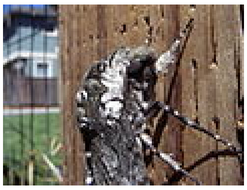
Traps

Adult *M. quinquemaculata* are most active in flight after dark.[10] Early studies found that the moths are attracted to blacklight, which is used as a lure in some traps. Although the traps can be used for research and the moths can be released after capture, traps like these have been suggested as a means of population control. However, one study found that the reduction in population was not strong enough to significantly impact population size.[17]

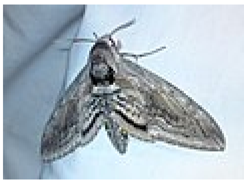
Images

Tomato hornworm larva

M. quinquemaculata diversity



Head detail



Live *M. quinquemaculata*

Tomato worm illuminated with UV on tomato plant

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Wikipedia

Integrated pest management

An IPM boll weevil trap in a cotton field (Manning, South Carolina).

Integrated pest management (IPM), also known as **integrated pest control (IPC)** is a broad-based approach that integrates practices for economic control of pests. IPM aims to suppress pest populations below the economic injury level (EIL). The UN's Food and Agriculture Organization defines IPM as "the careful consideration of all available pest control techniques and subsequent integration of appropriate measures that discourage the development of pest populations and keep pesticides and other interventions to levels that are economically justified and reduce or minimize risks to human health and the environment. IPM emphasizes the growth of a healthy crop with the least possible disruption to agro-ecosystems and encourages natural pest control mechanisms."[1] Entomologists and ecologists have urged the adoption of IPM pest control since the 1970s.[2] IPM allows for safer pest control.

The introduction and spread of invasive species can also be managed with IPM by reducing risks while maximizing benefits and reducing costs.[3][4][5]

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History

Shortly after World War II, when synthetic insecticides became widely available, entomologists in California developed the concept of "supervised insect control".[6] Around the same time, entomologists in the US Cotton Belt were advocating a similar approach. Under this scheme, insect control was "supervised" by qualified entomologists and insecticide applications were based on conclusions reached from periodic monitoring of pest and natural-enemy populations. This was viewed as an alternative to calendar-based programs. Supervised control was based on knowledge of the ecology and analysis of projected trends in pest and natural-enemy populations.

Supervised control formed much of the conceptual basis for the "integrated control" that University of California entomologists articulated in the 1950s. Integrated control sought to identify the best mix of chemical and biological controls for a given insect pest. Chemical insecticides were to be used in the manner least disruptive to biological control. The term "integrated" was thus synonymous with "compatible." Chemical controls were to be applied only after regular monitoring indicated that a pest population had reached a level (the economic threshold) that required treatment to prevent the population from reaching a level (the economic injury level) at which economic losses would exceed the cost of the control measures.

IPM extended the concept of integrated control to all classes of pests and was expanded to include all tactics. Controls such as pesticides were to be applied as in integrated control, but these now had to be compatible with tactics for all classes of pests. Other tactics, such as host-plant resistance and cultural manipulations, became part of the IPM framework. IPM combined entomologists, plant pathologists, nematologists and weed scientists.

In the United States, IPM was formulated into national policy in February 1972 when President Richard Nixon directed federal agencies to take steps to advance the application of IPM in all relevant sectors. In 1979, President Jimmy Carter established an interagency IPM Coordinating Committee to ensure development and implementation of IPM practices.[7]

Perry Adkisson and Ray F. Smith received the 1997 World Food Prize for encouraging the use of IPM.[8]

Applications

IPM is used in agriculture, horticulture, forestry, human habitations, preventive conservation and general pest control, including structural pest management, turf pest management and ornamental pest management.

Principles

An American IPM system is designed around six basic components:[9]

- **Acceptable pest levels**—The emphasis is on *control*, not *eradication*. IPM holds that wiping out an entire pest population is often impossible, and the attempt can be expensive and unsafe. IPM programmes first work to establish acceptable pest levels, called action thresholds, and apply controls if those thresholds are crossed. These thresholds are pest and site specific, meaning that it may be acceptable at one site to have a weed such as white clover, but not at another site. Allowing a pest population to survive at a reasonable threshold reduces selection pressure. This lowers the rate at which a pest develops resistance to a control, because if almost all pests are killed then those that have resistance will provide the genetic basis of the future population. Retaining a significant number of unresistant specimens dilutes the prevalence of any resistant genes that appear. Similarly, the repeated use of a single class of controls will create pest populations that are more resistant to that class, whereas alternating among classes helps prevent this.
- **Preventive cultural practices**—Selecting varieties best for local growing conditions and maintaining healthy crops is the first line of defense. Plant quarantine and 'cultural techniques' such as crop sanitation are next, e.g., removal of diseased plants, and cleaning pruning shears to prevent spread of infections. Beneficial fungi and bacteria are added to the potting media of horticultural crops vulnerable to root diseases, greatly reducing the need for fungicides.
- **Monitoring**—Regular observation is critically important. Observation is broken into inspection and identification.[10] Visual inspection, insect and spore traps, and other methods are used to monitor pest levels. Record-keeping is essential, as is a thorough knowledge of target pest behavior and reproductive cycles. Since insects are cold-blooded, their physical development is dependent on area temperatures. Many insects have had their development cycles modeled in terms of degree-days. The degree days of an environment determines the optimal time for a specific insect outbreak. Plant pathogens follow similar patterns of response to weather and season.
- **Mechanical controls**—Should a pest reach an unacceptable level, mechanical methods are the first options. They include simple hand-picking, barriers, traps, vacuuming and tillage to disrupt breeding.
- **Biological controls**—Natural biological processes and materials can provide control, with acceptable environmental impact, and often at lower cost. The main approach is to promote beneficial insects that eat or parasitize target pests. Biological insecticides, derived from naturally occurring microorganisms (*e.g.*—*Bt*, entomopathogenic fungi and entomopathogenic nematodes), also fall in this category. Further 'biology-based' or 'ecological' techniques are under evaluation.
- **Responsible use**—Synthetic pesticides are used as required and often only at specific times in a pest's life cycle. Many newer pesticides are derived from plants or naturally occurring substances (*e.g.*—nicotine, pyrethrum and insect juvenile hormone analogues), but the toxophore or active component may be altered to provide increased biological activity or stability. Applications of pesticides must reach their intended targets.

> Matching the application technique to the crop, the pest, and the pesticide is critical. The use of low-volume spray equipment reduces overall pesticide use and labor cost.

An IPM regime can be simple or sophisticated. Historically, the main focus of IPM programmes was on agricultural insect pests.[11] Although originally developed for agricultural pest management, IPM programmes are now developed to encompass diseases, weeds and other pests that interfere with management objectives for sites such as residential and commercial structures, lawn and turf areas, and home and community gardens.

Process

IPM is the selection and use of pest control actions that will ensure favourable economic condition, ecological and social consequences[12] and is applicable to most agricultural, public health and amenity pest management situations. The IPM process starts with monitoring, which includes inspection and identification, followed by the establishment of economic injury levels. The economic injury levels set the economic threshold level. That is the point when pest damage (and the benefits of treating the pest) exceed the cost of treatment.[13] This can also be an action threshold level for determining an unacceptable level that is not tied to economic injury. Action thresholds are more common in structural pest management and economic injury levels in classic agricultural pest management. An example of an action threshold is one fly in a hospital operating room is not acceptable, but one fly in a pet kennel would be acceptable. Once a threshold has been crossed by the pest population action steps need to be taken to reduce and control the pest. Integrated pest management employs a variety of actions including cultural controls such as physical barriers, biological controls such as adding and conserving natural predators and enemies of the pest, and finally chemical controls or pesticides. Reliance on knowledge, experience, observation and integration of multiple techniques makes IPM appropriate for organic farming (excluding synthetic pesticides). These may or may not include materials listed on the Organic Materials Review Institute (OMRI)[14] Although the pesticides and particularly insecticides used in organic farming and organic gardening are generally safer than synthetic pesticides, they are not always more safe or environmentally friendly than synthetic pesticides and can cause harm.[15] For conventional farms IPM can reduce human and environmental exposure to hazardous chemicals, and potentially lower overall costs.

Risk assessment usually includes four issues: 1) characterization of biological control agents, 2) health risks, 3) environmental risks and 4) efficacy.[16]

Mistaken identification of a pest may result in ineffective actions. E.g., plant damage due to over-watering could be mistaken for fungal infection, since many fungal and viral infections arise under moist conditions.

Monitoring begins immediately, before the pest's activity becomes significant. Monitoring of agricultural pests includes tracking soil/planting media fertility and water quality. Overall plant health and resistance to pests is greatly influenced by pH, alkalinity, of dissolved mineral and oxygen reduction potential. Many diseases are waterborne, spread directly by irrigation water and indirectly by splashing.

Once the pest is known, knowledge of its lifecycle provides the optimal intervention points.[17] For example, weeds reproducing from last year's seed can be prevented with mulches and pre-emergent herbicide.

Pest-tolerant crops such as soybeans may not warrant interventions unless the pests are numerous or rapidly increasing. Intervention is warranted if the expected cost of damage by the pest is more than the cost of control. Health hazards may require intervention that is not warranted by economic considerations.

Specific sites may also have varying requirements. E.g., white clover may be acceptable on the sides of a tee box on a golf course, but unacceptable in the fairway where it could confuse the field of play.[18]

Possible interventions include mechanical/physical, cultural, biological and chemical. Mechanical/physical controls include picking pests off plants, or using netting or other material to exclude pests such as birds from grapes or rodents from structures. Cultural controls include keeping an area free of conducive conditions by removing waste or diseased plants, flooding, sanding, and the use of disease-resistant crop varieties.[12] Biological controls are numerous. They include: conservation of natural predators or augmentation of natural predators, sterile insect technique (SIT).[19]

Augmentation, inoculative release and inundative release are different methods of biological control that affect the target pest in different ways. Augmentative control includes the periodic introduction of predators.[20][21][22][23][24] With inundative release, predators are collected, mass-reared and periodically released in large numbers into the pest area.[25][26][27] This is used for an immediate reduction in host populations, generally for annual crops, but is not suitable for long run use.[28] With inoculative release a limited number of beneficial organisms are introduced at the start of the growing season. This strategy offers long term control as the organism's progeny affect pest populations throughout the season and is common in orchards.[28][29] With seasonal inoculative release the beneficials are collected, mass-reared and released seasonally to maintain the beneficial population. This is commonly used in greenhouses.[29] In America and other western countries, inundative releases are predominant, while Asia and the eastern Europe more commonly use inoculation and occasional introductions.[28]

The sterile insect technique (SIT) is an area-wide IPM program that introduces sterile male pests into the pest population to trick females into (unsuccessful) breeding encounters, providing a form of birth control and reducing reproduction rates.[19] The biological controls mentioned above only appropriate in extreme cases, because in the introduction of new species, or supplementation of naturally occurring species can have detrimental ecosystem effects. Biological controls can be used to stop invasive species or pests, but they can become an introduction path for new pests.[30]

Chemical controls include horticultural oils or the application of insecticides and herbicides. A green pest management IPM program uses pesticides derived from plants, such as botanicals, or other naturally occurring materials.

Pesticides can be classified by their modes of action. Rotating among materials with different modes of action minimizes pest resistance.[12]

Evaluation is the process of assessing whether the intervention was effective, whether it produced unacceptable side effects, whether to continue, revise or abandon the program.[31]

Southeast Asia

The Green Revolution of the 1960s and '70s introduced sturdier plants that could support the heavier grain loads resulting from intensive fertilizer use. Pesticide imports by 11 Southeast Asian countries grew nearly sevenfold in value between 1990 and 2010, according to FAO statistics, with disastrous results. Rice farmers become accustomed to spraying soon after planting, triggered by signs of the leaf folder moth, which appears early in the growing season. It causes only superficial damage and doesn't reduce yields. In 1986, Indonesia banned 57 pesticides and completely stopped subsidizing their use. Progress was reversed in the 2000s, when growing production capacity, particularly in China, reduced prices. Rice production in Asia more than doubled. But it left farmers believing more is better—whether it's seed, fertilizer, or pesticides.[32]

The brown planthopper, *Nilaparvata lugens*, the farmers' main target, has become increasingly resistant. Since 2008, outbreaks have devastated rice harvests throughout Asia, but not in the Mekong Delta. Reduced spraying allowed natural predators to neutralize planthoppers in Vietnam. In 2010 and 2011, massive planthopper outbreaks hit 400,000 hectares of Thai rice fields, causing losses of about $64 million. The Thai government is now pushing the "no spray in the first 40 days" approach.[32]

By contrast early spraying kills frogs, spiders, wasps and dragonflies that prey on the later-arriving and dangerous planthopper and produced resistant strains. Planthoppers now require pesticide doses 500 times greater than originally. Overuse indiscriminately kills beneficial insects and decimates bird and amphibian populations. Pesticides are suspected of harming human health and became a common means for rural Asians to commit suicide.[32]

In 2001, scientists challenged 950 Vietnamese farmers to try IPM. In one plot, each farmer grew rice using their usual amounts of seed and fertilizer, applying pesticide as they chose. In a nearby plot, less seed and fertilizer were used and no pesticides were applied for 40 days after planting. Yields from the experimental plots was as good or better and costs were lower, generating 8% to 10% more net income. The experiment led to the "three reductions, three gains" campaign, claiming that cutting the use of seed, fertilizer and pesticide would boost yield, quality and income. Posters, leaflets, TV commercials and a 2004 radio soap opera that featured a rice farmer who gradually accepted the changes. It didn't hurt that a 2006 planthopper outbreak hit farmers using insecticides harder than those who didn't. Mekong Delta farmers cut insecticide spraying from five times per crop cycle to zero to one.

The Plant Protection Center and the International Rice Research Institute (IRRI) have been encouraging farmers to grow flowers, okra and beans on rice paddy banks, instead of stripping vegetation, as was typical. The plants attract bees and a tiny wasp that eats planthopper eggs, while the vegetables diversify farm incomes.[32]

Agriculture companies offer bundles of pesticides with seeds and fertilizer, with incentives for volume purchases. A proposed law in Vietnam requires licensing pesticide dealers and government approval of advertisements to prevent exaggerated claims. Insecticides that target other pests, such as *Scirpophaga incertulas* (stem borer), the larvae of moth species that feed on rice plants allegedly yield gains of 21% with proper use.[32]

See also

- Agroecology
- Agronomy
- Biodynamic agriculture
- Endangered arthropod
- Forest integrated pest management
- International Organization for Biological Control
- Pesticide application
- Professional Landcare Network (PLANET)
- Push-pull technology
- Soil contamination
- Sustainable agriculture

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